MONARDA RUSSELIANA (LAMIACEAE) IN KANSAS

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ABSTRACT

Recent field studies have resulted in the discovery of *Monarda russeliana* in Woodson Co., Kansas. The species has previously been reported in Kansas but as a misapplication of the name *M. russeliana* (which is now treated as *M. bradburiana*). A short review of the pertinent literature, description of the site of occurrence, photographs of the natural habitat, and close up of specimen are presented. The occurrence of *M. russeliana* in Missouri, which was examined as part of this study, is briefly discussed and refuted.

Steyermark (1963), apparently following Fernald (1944), used the name *Monarda russeliana* to refer to the species of Missouri and surrounding states now correctly known as *M. bradburiana*. While the mention of *M. russeliana* in Kansas may not have been directly stated, it was implied through use of overly broad statements ("surrounding states," etc.) and the misapplication of the name *M. russeliana* for *M. bradburiana*, a species also occurring in that state. A summary of this is presented in Yatskievych (1999), who correctly used the name *M. bradburiana* in place of the misapplied name *M. russeliana* in Missouri. Yatskievych further mentions that true *M. russeliana* is restricted to southeastern Oklahoma and adjacent portions of Arkansas and Texas, in effect excluding *M. russeliana* from both Missouri and Kansas. The distribution of *M. russeliana*, as mapped by Kartesz (2016), includes eastern Oklahoma, western Arkansas, northeast Texas, central Kentucky, northern Alabama, and Taney Co., Missouri (see endnote). Based upon the following specimen, we document the occurrence of *M. russeliana* in Kansas.

> **Kansas**. Woodson County. Woodson County State Lake (Lake Fagen), post oak savanna-slightly mesic woodland, upper rim of creek, above creek drainage, 8 Jul 2016, *Singhurst 21049* (BAYLU). Figure 1. Two populations were observed, one inside the park (37°47'36.97" N, 95°50'21.74" W) and one outside (37°47'33.52" N, 95°49'41.82" W, where the specimen was collected). Only one specimen was collected due to the few number of plants present.

The *Monarda russeliana* site is located near the northern tip of the crosstimbers vegetational region of Kansas (Schoewe 1949; see Fig. 1) in the Chautauqua Hills, which are continuous with the post oak-blackjack oak forests of Oklahoma (Woods et al. 2005), which in turn is continuous with the post oak savannah and cross timbers of northeast and north-central Texas (Correll & Johnston 1970). The geology is sandstone outcrops with sandy loam soils. At this time, this is the most northern known record of the species in the western portion of its distribution. Associated vegetation, particularly in Kansas, consists of *Quercus stellata*, *Quercus marilandica*, *Cornus drummondii*, *Rhus glabra*, *Viburnum rufidulum*, *Vitis* sp., *Smilax bona-nox*, *Schizachyrium scoparium*, *Andropogon virginicus*, *Chasmanthium latifolium*, *Tridens flavus*, *Scleria ciliata*, *Parthenocissus quinquefolia*, *Liatris squarrosa* var. *glabrata*, *Antennaria parlinii*, *Lespedeza* sp., *Elymus* sp., *Buchnera americana*,

Chamaecrista fasciculata, Lechea tenuifolia, Achillea millefolium, Asclepias verticillata, Erigeron sp., and *Stylosanthes biflora.*

Figure 1. *Monarda russeliana* in Woodson Co., Kansas (*Singhurst 21049*, BAYLU). Photo by J.R. Singhurst.

Figure 2. *Monarda russeliana* habitat in Kansas. Photo by J.R. Singhurst.

Comments on the occurrence of *Monarda russeliana* in Missouri

Kartesz (2016) currently maps *Monarda russeliana* from Taney County of southwest Missouri based upon *McReynolds 750675* (LSU) [a photo of the documenting specimen is online at <images.cyperfloralouisiana.com/images/specimensheets/lsu00090923.jpg>. We suggest that *McReynolds 750675* is *M. bradburiana*, based upon the ovate nature of the leaves and shortness (or lack) of petioles. *Monarda russeliana* has lanceolate leaves with petioles about 5 mm long. It appears that the original determination of this specimen as *M. russeliana*, based upon collection date, was made using Steyermark's Flora of Missouri (1963), where the name *M. russeliana* is misapplied.

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SISYRINCHIUM MINUS (IRIDACEAE) NEW TO ALABAMA

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ABSTRACT

Sisyrinchium minus (Iridaceae) is reported new for the vascular flora of Alabama from collections made from 1987 to 2015. Several of the localities are in the Blackland Prairie district and the species is regarded as native to Alabama, disjunct from its primary range to the west.

Recent collections from Alabama identified as *Sisyrinchium minus* Engelm. & A. Gray have led to the conclusion that the species has never been documented for the state before now. The taxon was not included in *Plant Life of Alabama* (Mohr 1901) and was apparently overlooked for inclusion in a recently published checklist for the state (Kral et al. 2011), despite a collection predating that publication by 24 years (Fig. 1). *Sisyrinchium minus* also has not been included in the Alabama Plant Atlas (Keener et al. 2016).

Sisyrinchium minus Engelm. & A. Gray
Voucher specimens. **USA. Alabama.** Marengo Co.: 2.5 air mi WSW of Demopolis, along N side of Lock and Dam Rd. 0.06 mi E of jct. with Gandy Ferry Rd, 32.511093° -87.88064°, 1 May 2012, *England 3431* (UWAL; VDB). Monroe Co.: 3.5 air mi WNW of Franklin, Haines Island Park at site of old Davis Ferry, boat landing, 31.72563° -87.46920°, 13 May 2015, *Keener 8842* with Davenport and Davison (UWAL); off Co. Rd. 17 at Haines Island Park, ca. 16 mi W of Beatrice, 31.725189° -87.47055°, 13 May 2015, *Davenport 5746* (SAMF). Sumter Co.: 2.8 air mi NE of Coatopa, along Mundy Rd. ca. 0.25 mi N of jct. with Co. Rd. 23, 32.507778° -88.029444°, 17 Apr 2010, *Keener 5808* with Duckworth (UWAL; MIN, duplicates to be distributed). Wilcox Co.: By Alabama Hwy 22 [5?], E side of Flatwood, 1 May 1987, *Kral 73815* (VDB, UWAL; duplicates to be distributed).

Sisyrinchium minus was originally described from the prairie region of Texas, where it apparently is native (Englemann & Gray 1845). It is one of three annual species [*S. rosulatum* E.P. Bicknell, *S. cernuum* (E.P. Bicknell) Kearney] currently recognized in the genus from North America north of Mexico (Cholewa & Henderson 2002). Since its description, discoveries have been made in neighboring and nearby states, including Arkansas, Oklahoma, Louisiana, and Mississippi (Kartesz 2015). Despite the recent discovery in Arkansas in 2007, it is considered native there because the only known population occurs along the margin of prairie flatwoods where other somewhat rare natives occur (T. Witsell, pers. comm.). In light of this, the species is regarded as an "S1" species, meaning it is tracked by the Arkansas Natural Heritage Commission as "Critically Imperiled" (NatureServe 2015). In Oklahoma, the first collection of *S. minus* was in 1981, where the habitat was recorded as a lawn weed on a college campus, suggesting an adventive occurrence (Taylor & Taylor 1987). It is unclear if the presence of *S. minus* in Louisiana and Mississippi represents native populations or adventive ones. *Sisyrinchium minus* has also been collected in southern California and North Carolina, where both populations are undoubtedly adventive (Kartesz 2015).

Figure 1. *Sisyrinchium minus* from Wilcox Co., Alabama (*Kral 73815*, UWAL).
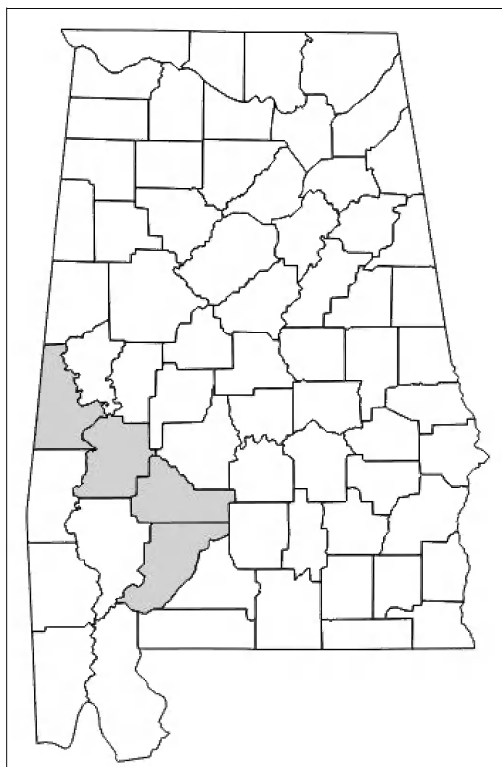
Figure 2. Map of Alabama with counties of documented *Sisyrinchium minus* populations in gray.

Figure 3. Capsules of *Sisyrinchium minus* (left) and *Sisyrinchium rosulatum* (right).

The Alabama populations of *Sisyrinchium minus* (Fig. 2) were discovered in moist habitats, including floodplains, mudflats, roadside ditches, and low fields. Several of the localities are in the Blackland Prairie physiographic district of Alabama, although not in an actual prairie and usually in circumneutral to slightly alkaline soils. The Marengo County population, which may have the most undisturbed habitat, was discovered under bald cypress (*Taxodium distichum*) along the edge of a seasonally flooded area of an embayment of the Tombigbee River. Also occurring at this locality was *Crassula aquatica*, a species reported in a previous paper (England 2013). The Blackland Prairie district of Alabama (and Mississippi) often harbors many unrelated species with a disjunct distribution between the Blackland Prairies of Texas and Arkansas and those of Alabama and Mississippi. Because a similar pattern is represented here, we believe *S. minus* should be treated as native in Alabama.

In the southeastern USA, *Sisyrinchium minus* could be confused with *S. rosulatum*, both of which are diminutive annuals. They can be easily separated by the shape of the capsules (Fig. 3). *Sisyrinchium rosulatum* produces globose capsules, while the capsules of *S. minus* are barrel-shaped.

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A NOTABLE RANGE EXTENSION FOR *SHINNERSIA RIVULARIS* (ASTERACEAE, EUPATORIEAE) IN TEXAS

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ABSTRACT

Previously known in Texas from only a few spring systems in Kinney, Uvalde, and Val Verde counties, the aquatic angiosperm *Shinnersia rivularis* is here reported from several sites in Kimble County, Texas, where it occurs in both submersed and emergent stands in and along the Llano and South Llano rivers. This report documents a range extension of ca. 140 km and the first known occurrence of the species in a river system of the Edwards Plateau natural region of Texas.

Despite estimates that put the total number of flowering plant species as high as 352,000 (Paton et al. 2008), surprisingly few of these species are well-adapted to the aquatic habitat. In Texas, the Rio Grande bugheal, *Shinnersia rivularis* (A. Gray) R.M. King & H. Rob., is the sole member of the large and diverse family Asteraceae that is a true hydrophyte, occurring as both submersed and emergent individuals in several spring systems in the southwestern part of the state. The species is easily recognized in the field by its distinctive growth habit and its abundantly produced, characteristic inflorescences (Fig. 1).
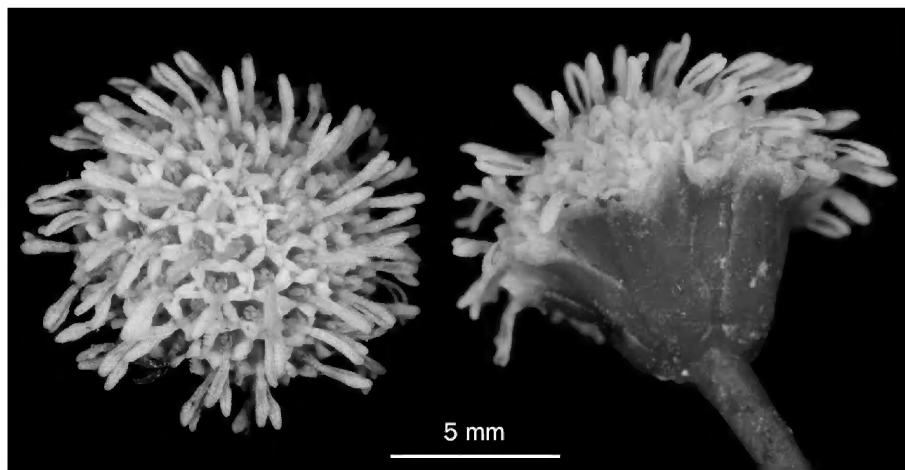

Figure 1. Capitula of *Shinnersia rivularis* from the South Llano River, Kimble Co., Texas (photo by D.E. Lemke).

Shinnersia rivularis was originally described (as *Trichocoronis rivularis*) by Asa Gray from specimens collected in northern Mexico by Lewis Edwards and Josiah Gregg (Gray 1849) and placed in his newly erected genus *Trichocoronis*, along with *T. wrightii*, a species of the Texas coastal plain (Turner et al. 2003). The species remained in *Trichocoronis* until segregated as a monotypic genus by King and Robinson (1970) on the basis of differences in inflorescence and corolla morphology, size of the involucre, and characteristics of the fruit and the pappus. Although many workers have continued to place the species in *Trichocoronis* (e.g., Correll & Correll 1975; Turner et al. 2003; Poole et al. 2007), Nesom recognized the genera as morphologically distinct in his Flora of North America treatments (Nesom 2006a, 2006b), and a recent molecular study (Tippery et al. 2014) also has provided data supporting the recognition of *Shinnersia* as distinct from *Trichocoronis*.

The first published record of *Shinnersia rivularis* (as *T. rivularis*) from Texas is in Asa Gray's *Plantae Wrightianae*, where the species was described as occurring "in the outlet of a spring tributary to the San Felipe; blooming profusely both above and beneath the surface of the water" in what is now Val Verde County (Gray 1852). Since that time, *S. rivularis* has also been collected from springruns in Uvalde and Kinney counties, Texas (Poole et al. 2007). The species is particularly abundant in the upper portion of San Felipe Creek below San Felipe Springs in the city of Del Rio (documented by numerous collections at TEX-LL) and at Soldiers Camp Springs along the Nueces River in western Uvalde County (Brune 1981), where it has been observed by the first author and collected by W.R. Carr (*Carr 18821*, TEX). The present report, based upon the specimens cited below, documents a range extension of approximately 140 km and the first report of the species from a river system, as opposed to a springrun, in the Edwards Plateau natural region of the state.

Voucher specimens. Texas. <u>Kimble Co.</u>: South Llano River State Park, near the day use area, 0.4 mi N of headquarters building, 11 Apr 2009, *Hansen 6388* (TEX); Junction City Park along the N bank of the South Llano River, ca. 150 yards downstream of dam spillway with *Salix, Melia, Platanus, Juglans, Justicia, Andropogon*, grasses, weeds, 30°29'25.58" N, 99°45'33.57" W, 7 Apr 2011, *Reed 3410* (TAMU); Junction City Park along the N bank of the South Llano River, ca. 150 yards downstream of dam spillway with *Bacopa, Ludwigia, Hydrocotyle, Eleocharis, Myriophyllum, Veronica*, 30°29'25.58" N, 99°45'33.57" W, 8 Apr 2011, *Reed 3411* with Lemke (TAMU).

In addition to the collections cited above from the South Llano River, *Shinnersia rivularis* has been observed and photographed downstream in the Llano River, a short distance below the confluence of the North and South Llano rivers.

In both the South Llano and Llano rivers, *Shinnersia rivularis* forms extensive mats of submersed and emergent plants (Figs. 2–4). As an emergent, the species has been found growing in association with *Justicia americana, Bacopa monnieri, Hydrocotyle umbellata, Ludwigia peploides, Veronica anagallis-aquatica*, and *Eleocharis* spp. When growing submersed, *S. rivularis* typically forms dense, tangled mats that are only sporadically punctuated by other submersed macrophytes, such as *Potamogeton illinoensis* or *Myriophyllum heterophyllum* (Fig. 5). In the Llano and South Llano rivers, flowering has only been observed in emergent individuals, in contrast to the situation at San Felipe Creek, where capitula are commonly produced beneath the water surface.

Figure 2. Habitat of *Shinnersia rivularis* in the Llano River, Kimble Co., Texas, below the confluence of the South Llano and North Llano rivers. Emergent plants can be seen in the left foreground and submersed plants in the right foreground (photo by D.E. Lemke).

Figure 3. Flowering individual of *Shinnersia rivularis* in the Llano River, Kimble Co., Texas. Only emergent plants were seen to flower at this locality (photo by D.E. Lemke).
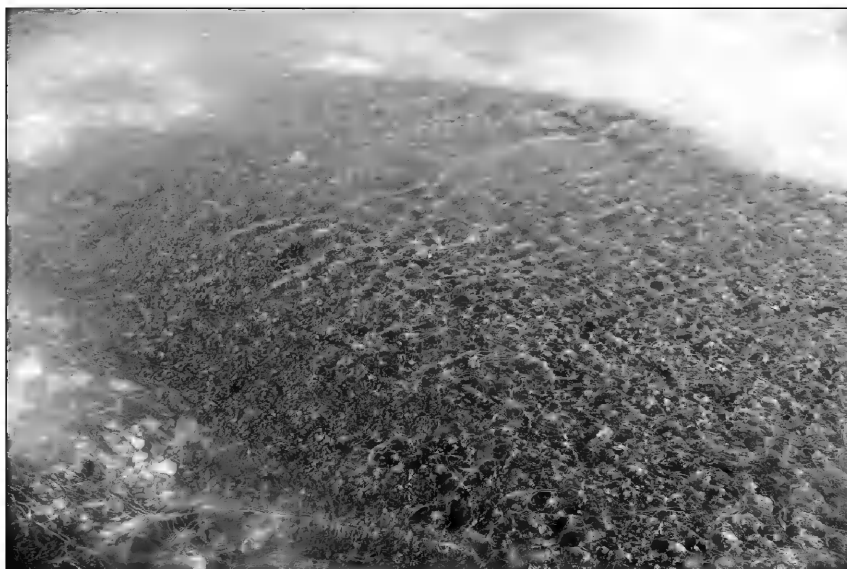
Figure 4. Dense submersed mat of *Shinnersia rivularis* in shallow water of the Llano River, Kimble Co., Texas (photo by D.E. Lemke).

Figure 5. Closeup of submersed mat of *Shinnersia rivularis* growing with *Potamogeton illinoensis* in the Llano River, Kimble Co., Texas.

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ZORNIA GEMELLA (FABACEAE) NEW TO FLORIDA

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ABSTRACT
Widely distributed in the New World, *Zornia gemella* ranges from South and Central America to the Caribbean. In the USA, it has previously been known only from southern Texas. We report the first known occurrence of this species from Florida.

While searching in Florida for additional localities of *Cyperus richardii* Steudel (cf. Carter et al. 2016), we encountered an unfamiliar *Zornia* with bifoliolate leaves, which we have identified as *Zornia gemella* Vogel. It is a species of tropical and warm temperate areas, ranging from South and Central America to the Caribbean and southern Texas (Mohlenbrock 1961, 1962). The only species of *Zornia* previously recorded for Florida is the southeastern endemic *Z. bracteata* J.F. Gmel. (Isley 1990; Wunderlin & Hansen 2011; Wunderlin et al. 2016) –– we report and describe our voucher collections of *Z. gemella*, documenting the first known occurrence of this species from the state.

Zornia gemella Vogel, Linnaea 12: 61. 1838.
Perennial herb. **Stems** trailing to decumbent, glabrous. **Leaves** palmately compound; leaflets 2, broadly elliptic to ovate below to lanceolate or lance-linear above, ± pellucid punctate. **Spikes** flexuous, bracteate, flowers mostly widely spaced; floral bracts lanceolate to narrowly elliptic, 6.0–7.5 x 1.3–1.7 mm, attached basally or slightly above the base and subpeltate, glabrous to ciliate and strigose. **Corolla** papilionaceous, basally included within the bracts but mostly exserted, yellow. **Loments** with (3–) 4–6 (–7) segments, oblong-linear, 8–15 x 1.8–2.0 mm, straight or curved, mostly exserted from bracts; segments ± square, 1.9–2.1 mm long, both hirtellous and with retrorsely barbed bristles. Figures 1 and 2.

USA. Florida. Hillsborough Co.: Alderman Ford Park, along E side of FL Hwy 39, 27.86974° N, 82.13712° W, infrequently mowed weedy border between athletic fields, disturbed sandy loam, occasional, 16 Dec 2015, *Carter 22597* with Mears (FLAS, MO, TROY, USF, VDB, VSC). Additional populations are expected at other ruderal sites in central and southern peninsular Florida.

Figure 1. *Zornia gemella* (*Carter 22597*, VSC); inset shows portion of inflorescence with bracts and exserted loments.

Both *Zornia bracteata* and *Z. gemella* have mostly prostrate to trailing stems. However, the bifoliolate leaves of *Z. gemella* (4-foliolate in *Z. bracteata*) and its much narrower and less conspicuous lanceolate to narrowly elliptic floral bracts (ovate to elliptic in *Z. bracteata*) are immediately obvious differences. The key below distinguishes these two species.

1. Leaves with 2 leaflets; floral bracts lanceolate to narrowly elliptic, 1.3–1.7 mm wide; loment with retrorsely barbed bristles and hirtellous; loments with (3–) 4–6 (–7) segments; loment segments ± square, 1.9–2.1 mm long .... **Zornia gemella**

1. Leaves with 4 leaflets; floral bracts ovate to elliptic, 3.5–7.1 mm wide; loment with retrorsely barbed bristles but otherwise glabrous; loments with 2–4 segments; loment segments lunulate, 3.4–4.2 mm long .... **Zornia bracteata**
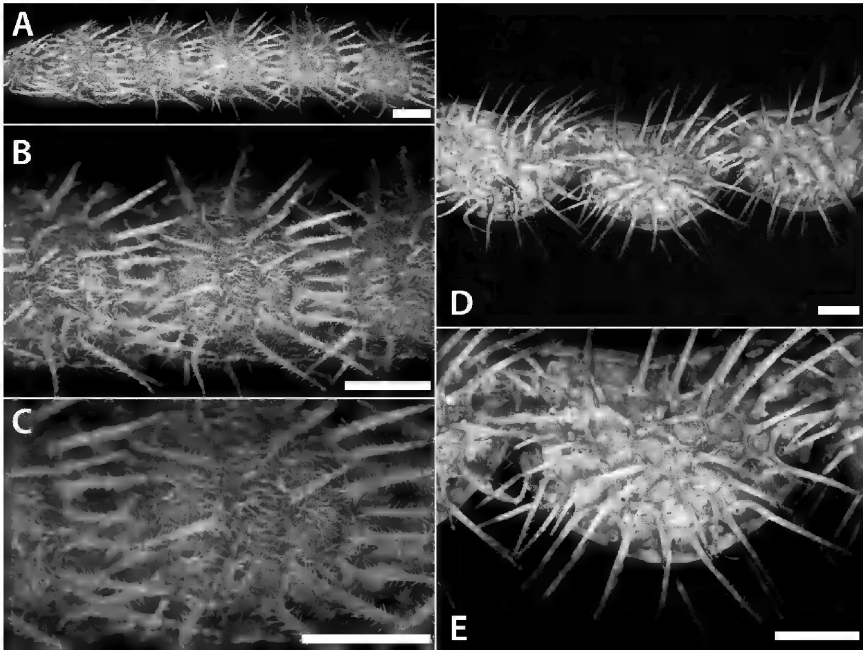

Figure 2. Loments of *Zornia gemella* (A–C) and *Z. bracteata* (D–E). **A.** Intact loment. **B.** Portion of loment showing three segments. **C.** Loment segment showing retrorsely barbed bristles and hirtellous pubescence. **D.** Portion of loment showing three segments. **E.** Loment segment showing retrorsely barbed bristles and absence of pubescence. All scale bars = 1 mm. A–C from *Carter 22597* (VSC); D–E from *Carter 17158* (VSC).

Source specimen of *Zornia bracteata* for loment photographs. **USA. Georgia.** Camden Co.: 30.78077 N 81.68903 W, 1.33 air mi S of Kingsland jct Hwy US 17 and GA Hwy 40, ca 0.1 mi W of railroad by Vacuna Rd, open sandy roadside, plants locally common, 18 Aug 2006, *Carter 17158* with Baker (VSC).

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NEW COMBINATIONS
FOR *HELIOTROPIUM POWELLIORUM* AND *HELIOTROPIUM PRINGLEI*
IN THE GENUS *EUPLOCA* (BORAGINALES: HELIOTROPIACEAE)

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ABSTRACT
We provide two new combinations needed for the treatment of *Euploca* (Boraginales: Heliotropiaceae) in a forthcoming volume of the Flora of North America North of Mexico: **Euploca powelliorum** (B.L. Turner) Feuillet & Halse, **comb. nov.**, from Texas and Mexico and **Euploca pringlei** (B.L. Rob.) Halse & Feuillet, **comb. nov.**, from Texas, Mexico, and Guatemala.

Morphological and molecular studies (Hilger & Diane 2003) provided evidence that *Heliotropium* sect. *Orthostachys* (R. Br.) G. Don (Brown 1810; Don 1838), *Schleidenia* Endl. (Endlicher 1839), and *Hilgeria* Förther (1998) constitute a separate genus whose earliest available name is *Euploca* Nutt. (Nuttall 1836). For more details and other new combinations, see Feuillet & Halse (2016).

Heliotropium powelliorum is closely related to *Euploca torreyi* (I.M. Johnst.) Halse & Feuillet (Johnston 1959; Feuillet & Halse 2016). It differs from *E. torreyi* by its longer inflorescences and the flowers more scattered and held nearly perpendicular to the inflorescence. *Heliotropium powelliorum* needs to be transferred to *Euploca*.

Euploca powelliorum (B.L. Turner) Feuillet & Halse, **comb. nov.** Basionym: *Heliotropium powelliorum* B.L. Turner, Lundellia 10: 7; figs. 1–3. 2007. TYPE: USA. Texas. Brewster Co.: 4 mi S [of Terlingua?] along Terlingua-Lajitas highway, 3500 ft, 28 Sep 1947, *B.H. Warnock 7576* (holotype LL [scan!]; isotypes: MEXU, SMU, SRSC, TEX [scan!]).

USA collections studied. Texas. Brewster Co.: Chisos Mtns area, Mesa de Anguila, 14 Jul 1937, *Warnock 991* (US), id., 14 Jul 1937, *Warnock 21126* (LL); Reed Plateau, 31 Mar 2007, *Weckesser 1012* (TEX), id., 4 Jul 1979, *Powell 3455* (TEX), id., 27 Jun 1978, *Powell 3335* (TEX); between Terlingua and Lajitas, 11 Sep 1961, *Correll & Johnston 24468* (LL), id., 14 Sep 1947, *Lundell 14766* (LL); 3 mi W of Terlingua, 24 Sep 1966, *Correll 33881* (LL!); W of Terlingua, 25 Jul 1973, *Henrickson 11292* (CSLA, NY). Presidio Co.: 3 mi SW of Shafter, 30 Jul 1945, *Muller 8469* (LL); E of Solitario Peak within the Solitario, on the Big Bend Ranch, 7 Jun 1975, *Butterwick & Strong 856* (TEX), id., 25 Sep 1975, *Butterwick & Lamb 1649* (TEX); Chinati Mtns, 5 mi S of Shafter, 5 Aug 1945, *Lundell & Lundell 14280* (LL); S side of Chinati Mtns, 14 Jul 1944, *Kinckley 3108* (CSLA, NY); Solitario, 24 May 1985, *Clark 1051* (TEX).

Heliotropium pringlei Robinson (1891) was described from Mexico, where it occurs from the state of Chihuahua to Chiapas and in Guatemala (Frohlich 1981). In 1982, it was collected in the southwestern corner of Cochise Co. Arizona (20 Sep 1982, *Soreng & Salazar 1895*, NMC, USC; as identified by Frohlich (Soreng 1984)).

Euploca pringlei (B.L. Rob.) Halse & Feuillet, **comb. nov.** Basionym: *Heliotropium pringlei* B.L. Rob., Proc. Amer. Acad. Arts 26: 170. 1891. LECTOTYPE (designated by Frölich 1981): MEXICO. **San Luis Potosi**. Thin soil of rocky hill, Las Canoas, 16 Jul 1890, *C.G. Pringle 3207* (GH; isolectotypes: BM, BP, BR(2) [scan BR0000006966782!], F105294 [photo F!, neg 51140], GOET, HBG, JE, LE, K 000478236 [scan!], LL(2) [2 scans!], M, MEXU, MO!, NY(2)!, P(2)!, RSA, S, TEX, UC, US 0051296 1! [scan!], W 350, WU). SYNTYPE (Robinson 1981): MEXICO. **Chihuahua**. Sta. Eulalia Mtns, 2 Oct 1886, *C.G. Pringle 1160* (GH).

The isolectotypes we have not seen are cited by Förther (1998). As far as we know, *Soreng & Salazar 1895* from Arizona, near Mexico and New Mexico borders is the only USA collection for this species.

Nine of the ten species of *Euploca* present in the USA occur at least in one of 3 states: Arizona, New Mexico, and Texas and are also in the flora of Mexico (Table 1). No *Euploca* species is endemic to the USA.

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We want to thank the curators who made our study of the specimens in their care possible (MO, NY, TEX, US). We are grateful to the editor for his review.

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Table 1. Distribution of the species of *Euploca* occurring in the USA. The usual abbreviations are used for USA states; CAm = Central America (more than one country, besides Mexico); SAm = South America; WI = West Indies (more than two islands).

	Arizona	New Mexico	Texas	other
E. confertifolia (Torr.) Feuillet & Halse			X	Mexico
E. convolvulacea Nutt.	X	X	X	AR, CA, CO, KS, NE, NV, OK, UT, WY; Mexico
E. fruticosa (L.) J.I.M. Melo & Semir	X	X	X	FL; Mexico
E. greggii (Torr.) Halse & Feuillet		X	X	Mexico
E. polyphylla (Lehm.) J.I.M. Melo & Semir				FL; Bahamas, SAm
E. powelliorum (B.L. Turner) Feuillet & Halse			X	Mexico
E. pringlei (B.L. Rob.) Halse & Feuillet	X			Mexico, Guatemala
E. procumbens (Mill.) Diane & Hilger	X		X	AR, FL, LA, MS; Mexico, CAm, SAm, WI
E. tenella (Torr.) Feuillet & Halse			X	AL, AR, GA, IA, IL, IN, KS, KY, MO, MS, OK, TN, WV?; Mexico
E. torreyi (I.M. Johnst.) Halse & Feuillet			X	Mexico
10 species	4	3	8	

DRABA RAMOSISSIMA (BRASSICACEAE) NEW TO ALABAMA

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ABSTRACT

Draba ramosissima (Brassicaceae) is reported new for the vascular flora of Alabama based on a 2015 Marshall County collection made from a population on a limestone bluff along the Tennessee River. The population represents a southern range extension for the species.

A recent collection of *Draba ramosissima* Desv. from Alabama is believed the be the first from the state. The taxon was not included in *Plant Life of Alabama* (Mohr 1901), a recently published comprehensive checklist for the state (Kral et al. 2011), or the Alabama Plant Atlas (Keener et al. 2016, a virtual herbarium data consortium of nine state herbaria).

Voucher. **USA. Alabama.** Marshall Co.: just SW of Fort Deposit Point, north bank of the Tennessee River at river mile 353.5, 34.428690° -86.332700°, 23 Apr 2015, *Dattilo s.n.* (UWAL). Figures 1–3.

The native distribution of *Draba ramosissima* is primarily centered in the southern Appalachians, where it is present in parts of Kentucky, Maryland, North Carolina, Tennessee, Virginia, and West Virginia (Kartesz 2015). When comparing the known distribution with Level III Ecoregions of the Continental United States (US EPA 2013), it can be found in parts the Blue Ridge, Ridge and Valley, Central Appalachians, and Southwestern Appalachians of the states listed above. While the species appears to be globally secure (G4), it has been assigned a rank S2 (Imperiled) by the North Carolina and Tennessee Natural Heritage programs (NatureServe 2015). The habitat for this species is often characterized by cliffs, bluffs, and rocky woods of limestone or shale (Al-Shehbaz et al 2010; Rollins 1993).

The habitat of the Alabama *Draba ramosissima* population is the edge of a limestone bluff with a sparse tree canopy primarily of Eastern Red Cedar. Subsequent surveys located a second location for the species several hundred feet to the west of the original observation, but no collection was made. In total, between 30 and 40 individual plants occur at the two sites. The discovery creates a new southernmost range extension for the species, approximately 180 km southwest of Polk Co., Tennessee. The population is approximately the same distance south-southwest of Dekalb Co., Tennessee, which is further north than Polk County.

The population of *Draba ramosissima* was observed during botanical surveys of limestone outcrop habitats between river miles 338-354 along the Tennessee River. Field surveys documented similar habitats at Black Bluff, Blue Rock Bluff, Clark Bluff, Honey Bluff, and Painted Bluff, but *D. ramosissima* was found only at the single area just southwest of Fort Deposit Point. It is expected

that the conservation status in Alabama will be assigned an S1 (Critically Imperiled) unless several other populations are discovered.

In recent years, systematic studies and subsequent treatments have transferred taxa formally classified in the genus *Draba* to *Abdra* and *Tomostima* (Al-Shehbaz 2012; Weakley 2015). In Alabama these include

Abdra brachycarpa (Nutt. ex Torr. & Gray) Greene (= *D. brachycarpa*),
Tomostima cuneifolia (Nutt. ex Torr. & Gray) Al-Shehbaz et al. (= *D. cuneifolia*), and
Tomostima reptans (Lam.) Al-Shehbaz et al. (= *D. reptans*)

with only *D. verna* L. remaining in the genus. With the addition of *D. ramosissma* to the Alabama flora, total number of *Draba* (sensu stricto) taxa in the state is two. The pair can be easily separated morphologically as *D. verna* is scapose with flat siliques while *D. ramosissma* produces several stem leaves and twisted siliques.

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Figure 1. *Draba ramosissima* from Marshall Co., Alabama (*Dattilo s.n.*, UWAL).

Figure 2. Habit of *Draba ramosissima* along limestone bluff, Marshall Co. Alabama.

Figure 3. *Draba ramosissima* stem base (left); flowers (right).

Figure 4. Alabama map showing Marshall Co., where the population of *Draba ramosissima* occurs.

ERYTHRANTHE DIMINUENS (PHRYMACEAE), A NEW SPECIES OF SECT. *SIMIOLUS* FROM SONORA

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ABSTRACT

Erythranthe diminuens Nesom, **sp. nov.**, is described from east-central Sonora, Mexico. It has fimbriate corolla margins and is a member of the group within sect. *Simiolus* that also includes *E. parvula*, *E. dentiloba*, and *E. chinatiensis*. The new species apparently is narrowly endemic, known only from the type collection.

Identification of recent collections from Sonora, Mexico –– in the Madrean Archipelago Biodiversity Assessment and Madrean Discovery Expeditions biotic inventory programs in Sonoran Sky Islands (MDE 2017) — brings to light a previously undescribed species of *Erythranthe*. It has a rhizomatous, mat-forming habit and fimbriate corolla margins and joins a group within sect. *Simiolus* (Nesom 2012) of three similar species from northwestern Mexico and the adjacent USA (Fig. 4).

ERYTHRANTHE DIMINUENS Nesom, **sp. nov.** **TYPE: MEXICO. Sonora.** Mpio. de Bacadéhuachi: Sierra de Bacadéhuachi, Rincón de Guadalupe, 16.5 km (air) ENE of Bacadéhuachi, Arroyo Campo los Padres (Río Riíto drainage), 29°50'40" N, 108°58'37" W, pine-oak forest, 1690 m, locally abundant herbaceous perennial on moist, shady bank, 31 Mar 2012, *A.L. Reina-G 2012-271* with Van Devender and Rice (holotype: TEX!; isotypes: ARIZ, MEXU, USON). Figure 1.

Similar to *Erythranthe parvula* in its fimbriate corolla margins, prostrate habit, and plesiogamous arrangement of stamens and stigma but different in its leaves consistently much smaller (2–4 x 2–4 mm vs 3–11 x 3–9 mm) and villous with flexuous, glandular hairs only on the upper surface (vs stiffly hispid-hirsute on both surfaces).

Perennial, rhizomatous, mat-forming. **Stems** prostrate, 2–10 cm, sometimes rooting at the nodes, minutely and sparsely stipitate-glandular. **Leaves** cauline, petiolate, blades broadly ovate to deltate, 2–4 mm x 2–4 mm (consistent in size, fide Thomas R. Van Devender, pers. comm.), venation not evident, adaxially densely villous with flexuous, broadly flattened, vitreous, gland-tipped hairs 0.2–1.0 mm long, abaxially dark purple and glabrous, margins serrate to denticulate with 2–4 teeth per side, apices acute to obtuse, bases truncate to cuneate, petioles 1–2 mm. **Flowers** axillary, 1–2 per node. **Fruiting pedicels** 4–20 mm, sparsely and minutely stipitate-glandular. **Fruiting calyces** cylindric-ovoid, 4–5 mm, closing, barely if at all nodding, moderately villous with gland-tipped hairs, lobes 5, acute-attenuate. **Corollas** yellow, red-dotted, tube-throat funnelform, 6–8 mm, exserted 4–5 mm beyond calyx margin, limb bilabiate, expanded 3–4 mm (pressed), lobes fimbriate. **Anther pairs** barely separated in level and essentially contiguous, stigma even with or very slightly above upper anther pair (plesiogamous, autogamous).

Known only from the type collection. The Sierra Bacadéhuachi (Wild Sonora 2017) has been considered a western ridge of the Sierra Madre Occidental or a separate Sky Island mountain range. The epithet alludes to the tiny leaves and flowers.
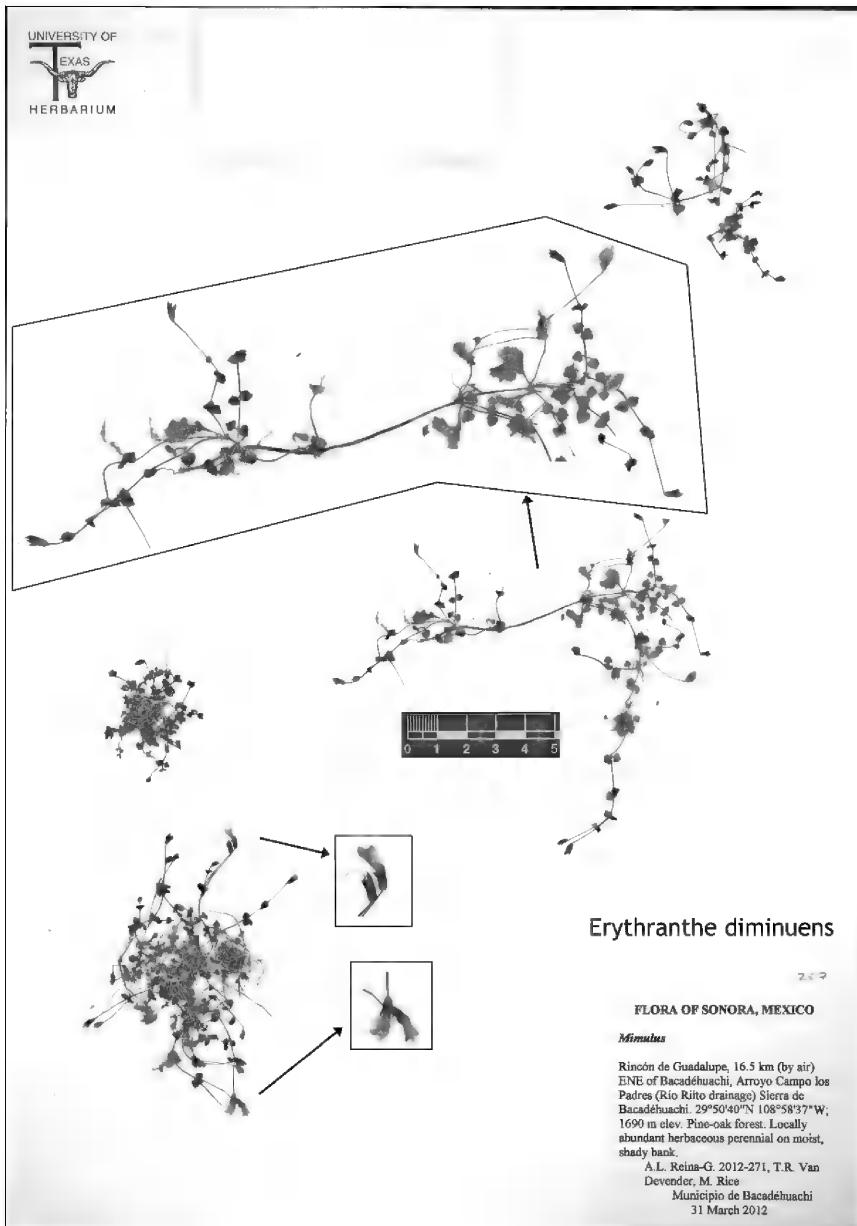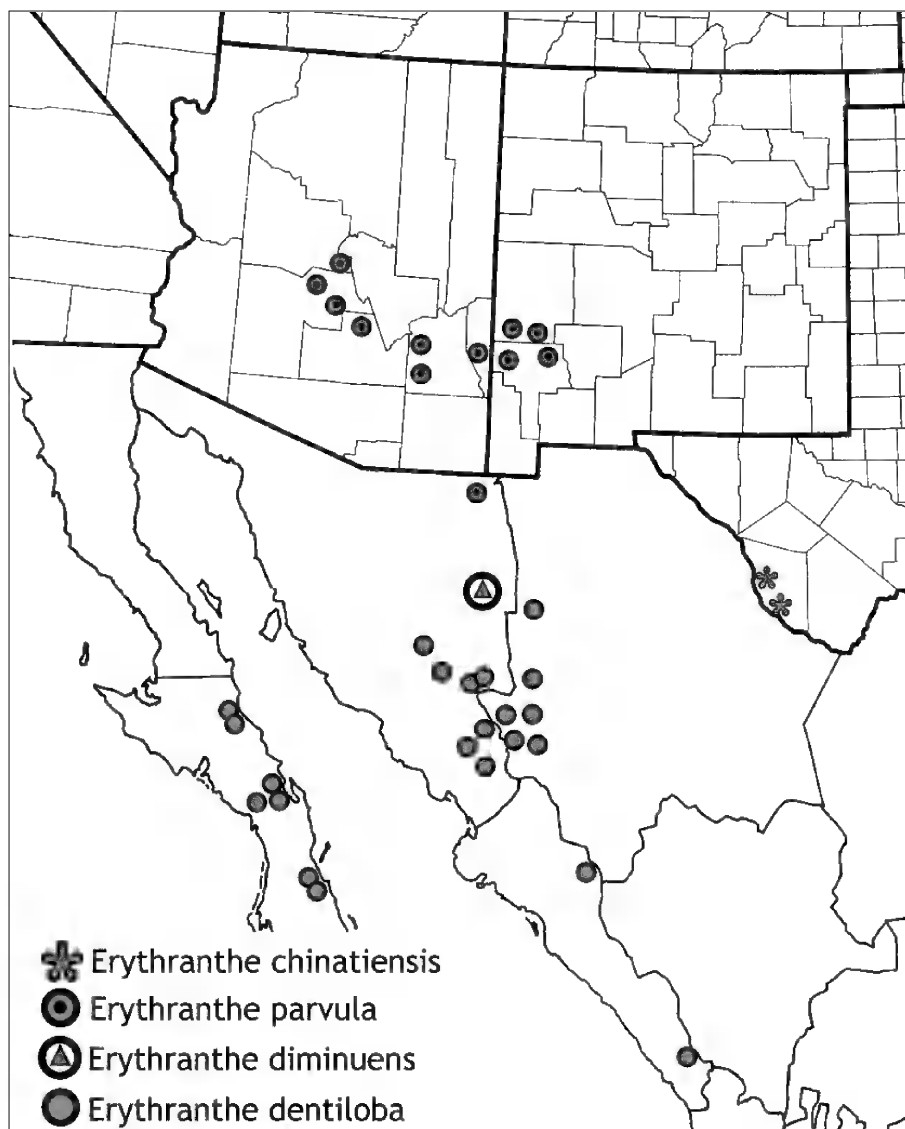
Figure 1. *Erythranthe diminuens*, holotype.

Figure 2. Distribution of *Erythranthe* sect. *Simiolus* species with fimbriate corolla margins. All occur in wet or seepy habitats; the two narrow endemics (*E. chinatiensis*, *E. diminuens*) are not evidently distinct as a pair.
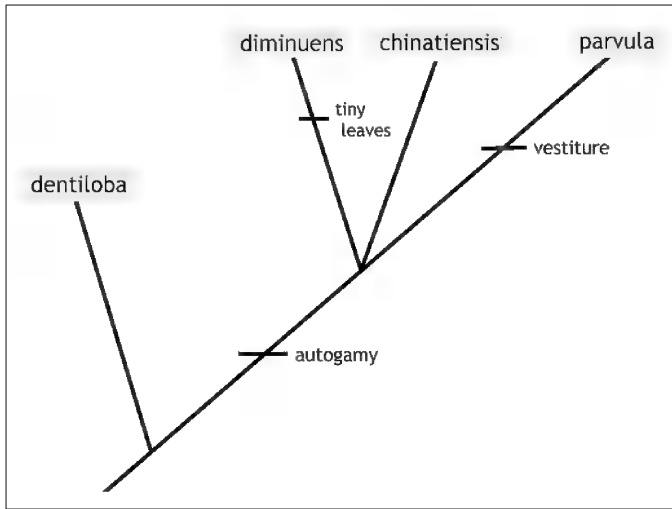
Figure 3. Informal phylogenetic hypothesis for the sect. *Simiolus* species with fimbriate corolla margins, assuming that allogamous breeding, villous-glandular vestiture, dentiloba-leaf size, and more than 1 flower per stem are plesiomorphic features. The scant cladistic resolution rests on the assumption that autogamy developed in the common ancestor of *E. dimiuens/chinatiensis/parvula* and was inherited. The vestiture of *E. parvula*, which occurs in no other species of *Erythranthe*, is assumed to be specialized.

The hispid-hirsute leaf vestiture of *Erythranthe parvula* sets it apart from the other species of the group with fimbriate corolla margins. Adaxial leaf surfaces of *E. diminuens* are densely glandular-villous with flexuous, flattened, and vitreous hairs; adaxial leaf surfaces of *E. dentiloba* and *E. chinatiensis* usually are glabrous but when a few hairs are produced, they are the same as in *E. diminuens*. The geography of *E. diminuens* (Fig. 2) suggests that it is more closely related to *E. dentiloba* than to the others (see further comments below), but *E. diminuens/E. chinatiensis*/E. *parvula* are autogamous (judging from the plesiogamous arrangement of stamens and stigma), compared to *E. dentiloba*, which is herkogamous and presumably allogamous. The key below distinguishes the four species.

1. Leaves glabrous on both surfaces or rarely sparsely glandular-villous adaxially; allogamous, stamen pairs at different levels, stigma above upper anther pair .... **Erythranthe dentiloba**

1. Leaves usually hairy at least adaxially; autogamous, both stamen pairs and the stigma at essentially the same level.

    2. Leaves hirsute adaxially with whitish, rigidly erect, minutely gland-tipped hairs; pedicels and distal stems stipitate-glandular .... **Erythranthe parvula**

    2. Leaves usually villous adaxially with flexuous, broadly flattened, vitreous, gland-tipped hairs; pedicels and distal stems glabrous or stipitate-glandular.

        3. Leaves 4–15(–22) mm x 4–15(–18) mm; glabrous to glandular-villous adaxially, abaxially green and glabrous; pedicels and stems glabrous .... **Erythranthe chinatiensis**

        3. Leaves 2–4 x 2–4 mm, adaxially glandular-villous, abaxially dark purple and glabrous; pedicels and stems sparsely stipitate-glandular .... **Erythranthe diminuens**

Erythranthe diminuens might be reasonably hypothesized to be a variant of *E. dentiloba* at the northernmost point of its range. Evidence supporting their distinction is summarized in the couplet below.

1. Leaves 2–10(–17) x 2–10(–20) mm; corolla tube-throats 5–7 mm, exserted 2–3 mm beyond the calyx margin, limb expanded 6–9 mm; herkogamous, presumably allogamous .... **Erythranthe dentiloba**

1. Leaves 2–4 mm x 2–4 mm (consistent in size); corolla tube-throats 6–8 mm, exserted 4–5 mm beyond the calyx margin, limb expanded 3–4 mm; plesiogamous, presumably autogamous
.... **Erythranthe diminuens**

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CORNUS ALTERNIFOLIA (CORNACEAE) IN TEXAS

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ABSTRACT
Cornus alternifolia is reported as new to Texas based upon a specimen collected in the rich hardwood-pine forest of northern Jasper County. The presence of the species in the state is disjunct from its nearest known occurrences in southern Mississippi and northwestern Arkansas but is considered native to the state. A list of species associated with the *Cornus* as well as a list of noteworthy (rare for Texas) southeastern species reported for the area are provided.

In the *Manual of the Vascular Plants of Texas* (Correll & Johnston 1970), the genus *Cornus* is treated as consisting of four species: *C. florida* L., flowering dogwood, native to the eastern one-third of the state and commonly used as a favored ornamental; *C. drummondii* C.A. Mey., rough-leaf dogwood, of the eastern half of the state (including the Edward's Plateau vegetational region and as an outlier in the eastern part of the (northern panhandle), *C. foemina* Mill., English dogwood, mostly of deep (far) east Texas; and *C. racemosa* Lam. of east Texas, now treated as a synonym of *C. foemina* (Turner 2003; Kartesz 2017). The present paper reports the occurrence of *C. alternifolia* L.f. (alternate-leaved dogwood) as part of the state's native flora.

Voucher. **Texas**. Jasper Co.: solitary shrub-like tree, 17.9 km (11.12 mi) at 015.08 degrees N of Jasper, sandy hardwood forest on bank of small perennial stream adjacent to a Catahoula sandstone outcrop, Campbell Global Property, WGS 84: 31.07548 N -93.94735 W, 14 Oct 2016, *Keith 1104* (BAYLU, SHST). Figures 1 and 2.

Cornus alternifolia occurs in the northeast and north-central USA (and adjacent Canada, Marie-Victorin 1964), south to South Carolina, Georgia, west Florida, Alabama, Mississippi, and Nebraska (Kartesz 2017). The Texas location is approximately 420 km (260 miles) from the nearest eastern location in Mississippi and 580 km (360 miles) from the nearest location to the north in Arkansas (both locations are based upon distributions in Kartesz [2017]).

The dogwood was initially discovered by Lewandowski in spring 2016 and collected by Keith in the fall (cited above). Peter Loos (in communication with Lewandowski) located another plant about 100 m downstream from the location cited, but the second was not found by Keith during the survey for additional specimens. It does seem highly unlikely that only a single plant exists. The vouchered tree is 4.6 m tall with a 5 cm dbh, with several stems sprouting from the base near the largest stem. There was no evidence of prior flowering, such as remnant inflorescences or fruit. The location is 1.6 km (1 mile) from the nearest occupied residence/building, indicating that the plant can reasonably be considered to be native.

Common associated species at the *Cornus* locality include *Quercus alba*, *Q. falcata*, *Fagus grandifolia*, *Prunus serotina*, *Ilex opaca*, *Ilex vomitoria*, *Acer rubrum*, *Ostrya virginiana*, *Vaccinium elliottii*, *Styrax grandifolius*, *Callicarpa americana*, *Symplocos tinctoria*, *Chasmanthium sessiliflorum*, *Dichanthelium commutatum*, *Athyrium felix-femina*, *Mitchella repens*, and numerous sedges (Cyperaceae). This part of Texas forms the southwestern terminus of the vast southeastern pine and pine-hardwood forests of the southeast USA and is characterized by an assemblage of rich woods species considered to be rare disjuncts and peripherals in Texas. Noteworthy species in this region (southern Sabine and northern Jasper and Newton counties) include *Houstonia purpurea*, *Verbesina walteri*, *Rudbeckia laciniata*, *Trillium ludovicianum*, *Prenanthes barbata*, *P. altissima*, *Amelanchier arborea*, *Phlox divaricata*, *Magnolia pyramidata*, *Stewartia malacodendron*, *Calycocarpum lyonii*, *Lyonia lucida*, and *Xanthorhiza simplicissima*. *Cornus alternifolia* joins the rare plant list.

Cornus alternifolia is a large shrub to small tree characterized by a multi-stemmed, upright spreading habit with layered, horizontal branching. The leaves are simple, alternate, and clustered toward the branch tips on short internodes, resulting in a whorled appearance. Leaves are medium to dark green and glabrous on the upper surface and gray-green to white on the lower surface. Leaf shape ranges from broadly elliptic to ovate with 4–6 pairs of pinnate arched primary nerves and acuminate apices. Petioles are light green to red and 2.5–5 cm long. Flat-topped inflorescences 5–9 cm wide and bearing tiny white 4-petaled flowers are borne in the leaf axils. In late summer, berry-like fruits to 0.4 cm diameter mature from green to bluish-black on reddish stalks.

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Figure 1. *Cornus alternifolia* (Cornaceae) in Jasper Co., Texas. Photo by Rick Lewandowski.

Figure 2. Leaf undersurfaces of same tree in Figure 1. Photo by Rick Lewandowski.

CUPANIOPSIS ANACARDIOIDES (SAPINDACEAE) NATURALIZED IN TEXAS

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ABSTRACT

Recent botanical work in Cameron Co., Texas, has resulted in the discovery of naturalized *Cupaniopsis anacardioides* in the understory of a *Sabal mexicana-Ebenopsis ebano* forest in a Nature Conservancy preserve. The population includes 30-40 plants of varying age classes from mature to seedling trees.

Cupaniopsis (Sapindaceae) is a genus of about 67 species known from Australia, New Guinea, and nearby islands of Micronesia, New Caledonia, and eastern Indonesia (Morat et al. 2012; Reynolds 1985; Hyland et al. 2010). *Cupaniopsis anacardioides* (carrotwood, tuckeroo) is native to Australia, Indonesia, and Papua New Guinea and has been introduced to the USA –– California (Lockhart et al. 1999), Florida (Oliver 1992), Hawaii (Oʻahu, Frohlich & Lau 2010; Maui, Starr & Starr 2011; and Kauai, Starr & Starr 2015). Establishment in the USA apparently has resulted from its usage in the subtropical nursery trade during the 1950s and early 1960s. The present paper documents the occurrence of the species to Texas, based on the following specimen.

TEXAS. Cameron Co.: Nature Conservancy Southmost Preserve 0.7 mi S on Southpoint Rd. from junction of FM 1419 and Southpoint Rd. Resaca (15°51'04", 97°23'52"), near Alabama-Arkansas Colonia (South Point), old river channel (resaca) of the Rio Grande, 9 Dec 2015, *Singhurst 21,031* with D. Allen and M. Pons (BAYLU).

The Texas locality is in the lower Rio Grande Valley in an old river channel (*resaca*) that accumulates water during rainy periods. The population (Figs. 1 and 2) occurs in the understory of a *Sabal mexicana-Ebenopsis ebano* forest and includes 30-40 plants of varying age classes, from mature to seedling trees. This community is a subtropical, evergreen forest dominated by a mixture of subtropical and temperate riverine species with scattered *Sabal mexicana*. In addition, associated vegetation includes *Fraxinus berlandieriana, Celtis laevigata, Ulmus crassifolia, Ebenopsis ebano (= Pithecellobium ebano), Leucaena pulverulenta*, and *Ehretia anacua*. Typical shrubs include *Sideroxylon celastrinum (= Bumelia celastrina), Malvaviscus arboreus var. drummondii (= Malvaviscus drummondii)*, and *Celtis pallida*.

Figure 1. *Cupaniopsis anacardioides* in understory of a *Sabal mexicana-Ebenopsis ebano* forest Cameron Co., Texas. Photo by Jason Singhurst, 9 December 2015.

Figure 2. *Cupaniopsis anacardioides* in understory of *Sabal mexicana-Ebenopsis ebano* forest, Cameron Co., Texas. Photo by Jason Singhurst, 9 December 2015.

Cupaniopsis anacardioides fruits are consumed by birds and seeds dispersed far from parent plants (Lockhart et al. 1999), which likely are the source and establishment of Gulf intercoastal island populations of *C. anacardioides* adjacent to the Florida coastline. Distributional expansion of *C. anacardiodes* in Florida has been well documented (Wunderlin et al. 1996; Wunderlin & Hansen 2008). The species was placed on the noxious weed list of Florida in 1999 (Langeland & Enloe 2001), but seed dispersal by birds frustrates efforts to control the spread of the species (Langeland & Burks 1998). In Florida, consumption of fruits by fish crows (*Corvus ossifragus*) is particularly noteworthy because of the exaggerated seed dispersal from inland feeding sites to coastal islands, which threatens coastal communities (Lockhart et al. 1999), potentially mangrove stands. Discussion of frugivory and dispersal of coastal exotic fruiting species by native passerines is discussed in Mink et al. (2015).

Known areas of *Cupaniopsis anacardioides* distribution in Florida receive a minimal rainfall of 122 cm/year (= 48 inches/year) (Spatial Climate Analysis Service –– PRISM 2015). Precipitation values for the Texas coast below Corpus Christi to South Padre Island averages 68.1 cm/year (= 26.8 inches /year), but rainfall for the upper (northern) Gulf coast can exceed 153.5 cm/year (60.4 inches/year), which might be favorable for the species should it reach the area and tolerate the cooler temperatures.

Masterson (2007) cited temperature as the probable key factor limiting the spread of *Cupaniopsis anacardioides* in north Florida, with -6˚ C (value from Lockhart 2006) as the lower

lethal for the species, although test specimens have survived winter temperatures as low or lower. This suggests to us that there would be little or no impediment to spread of the species northward along the Texas coast, where average minimum temperatures are 15.0˚ C to 19.4˚ C (Spatial Climate Analysis Service –– PRISM 2015).

Texas Nature Conservancy plans on removal of *Cupaniopsis anacardioides* from the preserve but current efforts are on eradicating *Megathyrsus maximus* (guinea grass), *Pennisetum ciliare* (buffelgrass), *Ricinus communis* (castor bean), and other exotics more locally aggressive than *C. anacardioides.*

ACKNOWLEDGEMENTS

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RUBUS BEAMANII, A NEW NAME FOR *RUBUS VAGUS* L.H. BAILEY, A GLANDULAR DEWBERRY DESCRIBED FROM KALAMAZOO COUNTY, MICHIGAN, AND RECENTLY DISCOVERED IN OHIO

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ABSTRACT
The recent discovery of *Rubus vagus* L.H. Bailey at Camp Ravenna Joint Military Training Center in Portage and Trumbull County, Ohio, has highlighted a seldom-seen species of North American *Rubus* that, for 70 years, has been illegitimately named. We propose a valid name for it: **Rubus beamanii** Widrlechner & Riley, **nom. nov.**, honoring Professor John Beaman (1929-2015). A key to the glandular dewberries of Ohio and surrounding states is included as an aid to distinguishing *R. beamanii* from the other glandular dewberries encountered in the region.

In the early 1940s, the genus *Rubus* was extensively collected in Kalamazoo Co., Michigan, by Clarence and Florence Hanes and Fred Rapp. Their specimens were shared with Liberty Hyde Bailey for identification in preparation for the publication of "The Flora of Kalamazoo County, Michigan" (Hanes & Hanes 1947). In that book, Bailey described 14 new species of *Rubus*, including six new members of a group he referred to as sect. *Flagellares* (L.H. Bailey) L.H. Bailey. As noted by Reveal (2014), the correct name for this diverse section is actually the earlier sect. *Procumbentes* (Rydb.) L.H. Bailey. Hereafter, we refer to members of this section as dewberries.

The recent Flora North America treatment (Alice et al. 2014) treats the dewberries, which vary widely in their morphology, phenology, habitat preferences, and ploidy levels, with more than 50 species recognized in the most recent sectional revision (Davis et al. 1968), as a single, highly polymorphic taxon, *Rubus flagellaris* Willd., downplaying studies that have examined the diverse, polyploid cytogenetics and breeding biology of dewberry taxa (Einset 1947; Thompson 1961, 1962, 1997).

In the north-central USA, dewberries are widely distributed and are typically found in old fields, prairies, savannas, and woodlands. Most dewberry taxa in this region lack stipitate glands. For example, of the seven dewberry species native to Minnesota, only *Rubus ithacanus* bears stipitate glands (Widrlechner & Smith 2008), and of the 11 species native to Missouri, only *R. deamii* and *R. leviculus* bear them (Widrlechner 2013). As a group, the glandular dewberries of the region are poorly understood and have been infrequently collected. In Iowa, no glandular dewberry populations have been well-documented since the 1950s.

In July 2014, Riley discovered a glandular dewberry population at Camp Ravenna Joint Military Training Center (Camp Ravenna) located on the Trumbull Co., Ohio, side of the 8775-hectare facility. This distinct, eye-catching dewberry was found growing in loamy, well-drained soil on a small rise on the edge of a mature swamp woods (flatwoods) dominated by *Quercus palustris*

and *Quercus bicolor*. There, the population encompassed about 80 m^2. Its low-arching, tip-rooting primocanes are densely covered with stipitate glands (Fig. 1), which give the canes and petioles a purplish appearance that, coupled with its leaves of mostly five leaflets, superficially resembles *R. trivialis* Michx. *Rubus trivialis*, or southern dewberry, is a state-endangered species in Ohio with only one extant population found along the banks of the Ohio River in Clermont County and a single known historical collection from 1916 in Hamilton County (ODNR 2016). The probability of this new find in northeast Ohio being *R. trivialis* seemed quite low, which motivated Riley to contact Widrlechner. Riley collected numerous specimens from this site in 2014 and deposited them at ISC and OS (abbreviations follow Thiers et al. 2016).

In September 2015, while walking along an abandoned railroad track through a mature, dry-mesic woods consisting primarily of *Quercus alba* and *Q. rubra* at Camp Ravenna, Riley found a second, smaller (18 m^2) population of this same glandular dewberry, on the Portage County side of the post, located 2.6 km southwest of the initial Trumbull County site. Several voucher specimens were made from this second population. These specimens, like those collected in 2014, are housed at ISC and OS.

Upon examination of numerous photographs depicting many of this dewberry's morphological traits, in addition to petiole and pedicel measurement data, Widrlechner concluded that what Riley had found most closely resembled *R. vagus* L.H. Bailey, based on the sectional key of Davis et al. (1968). *Rubus vagus* was among the six dewberry species that Bailey published in Hanes & Hanes (1947). However, during further investigation of this name, Widrlechner discovered that *R. vagus* was a later homonym and thus illegitimate, because *R. vagus* had been validly published earlier by W.O. Focke (1899) to name an Old World blackberry. The illegitimacy of *R. vagus* L.H. Bailey was independently noted by Alice et al. (2014).

We provide here a new name for *Rubus vagus* L.H. Bailey and present a key summarizing its distinctions (including the glandular dewberry populations found at Camp Ravenna) from other glandular dewberries known from Ohio and nearby states. Our intent for doing so is four-fold. First, it allows us to honor a distinguished botanist and educator who inspired many plant scientists throughout his long career. Second, it gives field botanists in the North Central region a quick identification tool for distinguishing among glandular dewberries. Third, it allows a valid name to be assigned for a potentially globally rare species that is likely deserving of protection in Michigan and Ohio, the only two states in which this species has been found and accurately verified. And finally, it sets the stage for future studies of this group, ones that can bring together phenotypic, cytological, and genetic analyses to develop a clearer picture of all the eastern North American glandular dewberries.

Rubus beamanii Widrlechner & Riley, **nom. nov.** *Rubus vagus* L.H. Bailey [nom. illeg.], Flora of
    Kalamazoo County, Michigan, 148, illus. 149. 1947 (non *Rubus vagus* Focke 1899). **TYPE:**
    USA. Michigan. Kalamazoo Co.: Alamo Township, Section 7, 30 Jul 1942, *C.R. Hanes 1712*
    (holotype: BH!). (Figures 2-4)

Representative collections. Michigan. Kalamazoo Co.: Section 7, Alamo Twp., moist woods, *C.R. Hanes 1773*, 11 Jun 1943 (BH, WMU), *C.R. Hanes 1773x*, 6 Aug 1943 (BH, WMU). (The WMU specimens include F.N. Hanes as a second collector.) **Ohio.** Portage Co.: SE ¼ Windham Twp., rare; small, local, native population with low-arching, tip-rooting primocanes growing on abandoned railroad ballast within mature mesic oak woods where plants receive half sun at most, SW of Ramsdell Quarry, Camp Ravenna Joint Military Training Center, Ravenna, 14 Sep 2015, *B.P. Riley 3318* (OS); *ibid, B.P. Riley 3319* (ISC). Trumbull Co.: SW ¼ Braceville Twp., small, local, non-fruiting population consisting of one individual with low arching, tip-rooting canes growing on wet-moist, semi-shaded edge of mature wet woods, S edge of 50-foot wide clearing,

North of Group 7 igloo block, Camp Ravenna Joint Military Training Center, Newton Falls, 17 Jul 2014, *B.P. Riley 3037* (OS); SW ¼ Braceville Twp., rare; rather large, local, fruiting population with low-arching, tip-rooting canes growing on slightly elevated, loam, acidic soil on W edge of mature pin oak flatwoods, N of Group 7 igloo block, Camp Ravenna Joint Military Training Center, Newton Falls, 21 Jul 2014, *B.P. Riley 3038* (OS); *ibid*, 29 Jul 2014, *B.P. Riley 3039* (ISC) (Figures 1, 5); *ibid*, 6 Aug 2015, *B.P. Riley 3320* (OS); *ibid, B.P. Riley 3321* (ISC).

We have been unable to confirm/document additional populations of *Rubus beamanii*. County distribution maps for this species show records for Monroe Co., Wisconsin (Kartesz 2015; USDA-NRCS 2016), and Clare Co., Michigan (Kartesz 2015), and we have examined likely "candidate" specimens from both counties, including *Davis 8745* (CM) from Clare County (based on its citation in Davis et al. 1968) and *Ugent s.n.* (WIS) from Monroe County (based on its annotation by A.M. Fuller as "could be *R. vagus*, Bailey"). However, both of those collections are samples of the more common mounding dewberry, *R. ithacanus*.

We have selected the epithet "*beamanii*" in honor of the late John Homer Beaman (1929-2015), Professor Emeritus of Botany at Michigan State University (MSU). Widrlechner took his first college plant taxonomy course from Professor Beaman in 1975 and was one of many students he inspired to continue their studies of plant systematics and evolution. Given Professor Beaman's long and productive career at MSU, aptly described by Clark & Donoghue (2005) and summarized by JSTOR (2016), and his interests in both plant conservation and field work, we feel that it is particularly fitting to give this epithet to an uncommon, native species originally described from Michigan.

To assist in identifying *Rubus beamanii*, we present the following key along with pertinent observations about the habitats and morphology of the glandular dewberries treated in the key.

Key to glandular dewberries of Ohio and surrounding states

1. Basal portion of canes ≥4 mm in diameter (often much stouter); plants forming a mounding tangle, only the terminal third to half of the canes trailing.

  2. Prickles on canes both broad-based and aciculate (needle-like), of varying lengths and strengths, 7–20+ per cm of cane .... **Rubus biformispinus** Blanchard
  2. Prickles on canes uniformly broad-based, 0–6 per cm of cane.

    3. Prickles on canes 0-4 per cm, inflorescence generally racemose, but sometimes ascendate (long-pedicellate, especially the more basal flowers) or (rarely) corymbose, with 5–15 (–20) flowers
    .... **Rubus ithacanus** L.H. Bailey
    3. Prickles on canes 2–6 per cm, inflorescence ascendate with ≤6 flowers
    .... **Rubus exsularis** L.H. Bailey

1. Basal portion of canes ≤5 mm in diameter; plants low-arching to prostrate.

  4. Inflorescences predominantly 1-flowered (rarely up to 3 flowers).

    5. Central leaflet of primocane leaves wide-ovate, with a cordate base   **Rubus centralis** L.H. Bailey
    5. Central leaflet of primocane leaves elliptic, with a cuneate to rounded base
    .... **Rubus leviculus** L.H. Bailey

  4. Inflorescences predominantly 3–10 (–15)-flowered (1-flowered inflorescences may be present on weak canes or near cane tips).

6. Canes bearing stipitate glands.

    7. Inflorescences ascendate; margin of primocane leaves irregularly serrate to dentate, base of central leaflets rounded .... **Rubus profusiflorus** L.H. Bailey
    7. Inflorescences racemiform; margin of primocane leaves finely serrate, base of central leaflets subcordate .... **Rubus beamanii**

6. Canes lacking stipitate glands.

    8. Primocane leaflets softly pubescent beneath.

        9. Primocane leaves predominantly 3-foliolate, central leaflet ≤7 cm long and 4.5 cm wide .... **Rubus deamii** L.H. Bailey
        9. Primocane leaves either 5-foliolate or a mixture of 3 and 5-foliolate, central leaflet ≥7 cm long and 4.5 cm wide .... **Rubus invisus** (L.H. Bailey) Britt.

    8. Primocane leaflets thinly pubescent to glabrous beneath.

        10. Primocane leaves 3-foliolate, central leaflet wide-elliptic to rhomboid, abruptly shouldered ....**Rubus kentuckiensis** L.H. Bailey
        10. Primocane leaves either 3- or 5-foliolate, central leaflet ovate, gradually acuminate .... **Rubus depavitus** L.H. Bailey

Relatively little is known about the habitat preferences of most of the 11 glandular dewberries keyed here. Among this group, associations with dry, sandy woodlands and open edges and roadsides are probably the most common, although all the well-described sites for *Rubus profusiflorus* are of sterile sands or sand prairies. *Rubus beamanii* differs somewhat from this tendency in that has typically been found in more mesic oak woodlands. Of the other 10 glandular dewberries, only *R. ithacanus* is regularly found in such settings (Widrlechner & Smith 2008).

Rubus beamanii produces relatively thin, whip-like primocanes that are low-arching to prostrate, quite unlike the large, mounding canes of *R. biformispinus*, *R. exsularis*, and *R. ithacanus*. Of 7 other low-arching to prostrate dewberries, only *R. profusiflorus* and some populations of *R. leviculus* typically share *R. beamanii*'s trait of bearing stipitate glands on their primocane axes. Remarkably, the protologue of *R. vagus* (Hanes & Hanes 1947) indicated that its canes "are free of glands," in direct conflict with the holotype, which clearly bears many stipitate glands (Figure 4).

When comparing primocane leaves, *Rubus beamanii* bears predominantly 5-foliolate leaves, with elliptic-ovate to elliptic central leaflets, most closely resembling *R. depavitus* and *R. invisus* in general form. However, the primocane leaves of *R. depavitus* are thinly pubescent to glabrous beneath, in contrast to the softly-pubescent undersides of the leaves of *R. beamanii* (and *R. invisus*). The central leaflets of *R. profusiflorus*, while sometimes ovate to elliptic, have a jagged appearance, with rough, 2 to 4 mm long teeth at a density of about 2 to 3 teeth per cm. The edges of *R. beamanii*'s central leaflets are finely serrate, with 0.5 to 2 mm long teeth at a density of about 4 to 5 per cm.

The most notable feature of floricane morphology of *Rubus beamanii* is its racemiform inflorescences (the longest ≤18 cm), typically bearing 7 to 10 (sometimes up to 15) flowers on relatively uniform pedicels (the longest ≤3 cm), most not subtended by leaflets (Figures 3, 5). Of the dewberries keyed here, only *R. biformispinus* and R. ithacanus typically bear racemose inflorescences, but they are often much longer both in overall and pedicel length. The remaining taxa in this key bear ascendate inflorescences with flaring pedicels, varying greatly in length, the most basal ones sometimes exceeding 8 cm in length.

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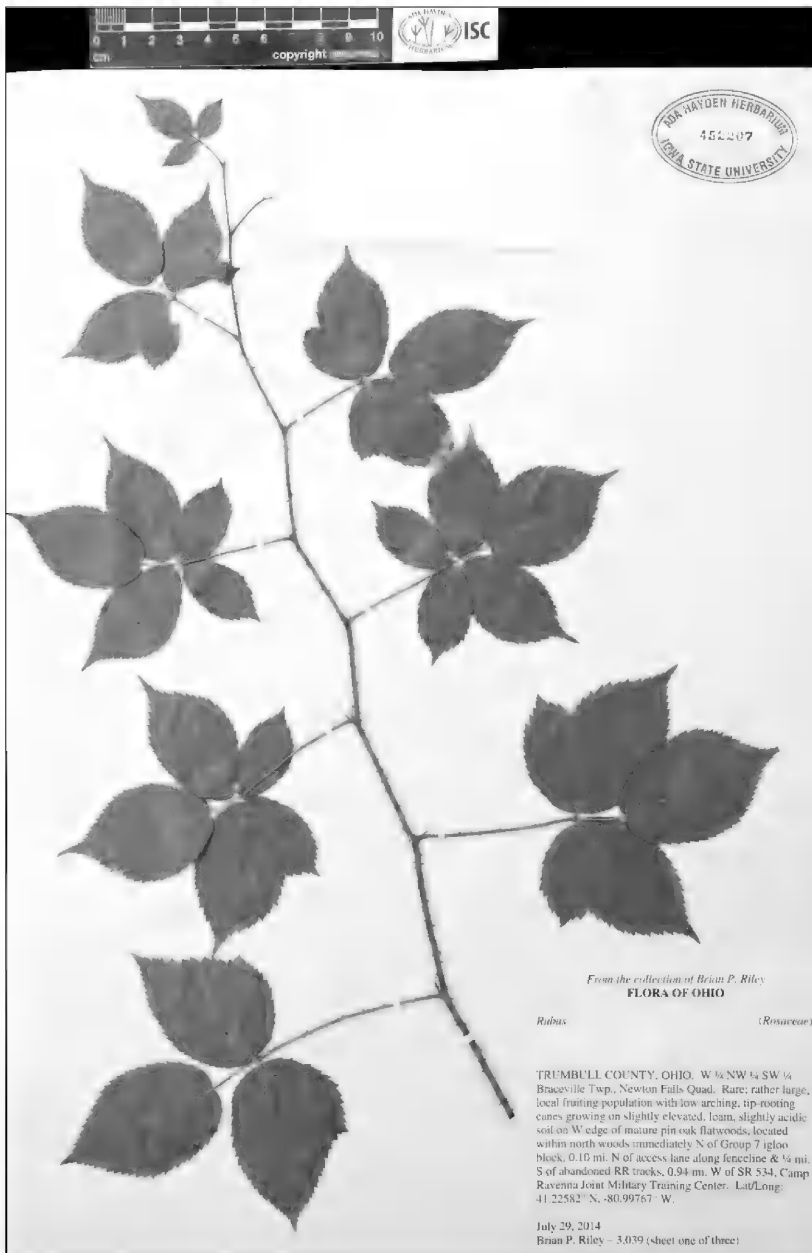Figure 1. *Rubus beamanii* primocane from Camp Ravenna in Trumbull Co., Ohio, July 2014.

Figure 2. A primocane from the holotype of *Rubus vagus*.

Figure 3. A floricane from the holotype of *Rubus vagus*.

Figure 4. Close-up of a primocane from the holotype of *Rubus vagus*, showing stipitate glands on its cane and petioles.

Figure 5. *Rubus beamanii* floricane from Camp Ravenna in Trumbull Co., Ohio, July 2014.

DACRYODES TALAMANCENSIS (BURSERACEAE), LA SEGUNDA ESPECIE DEL GÉNERO PARA AMÉRICA CENTRAL

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RESUMEN
Dacryodes talamancensis D. Santam. & Aguilar, **sp. nov.**, de los bosques montañosos de la Cordillera de Talamanca en territorio costarricense, es descrita e ilustrada. Esta corresponde a la segunda especie de *Dacryodes* para América Central.

ABSTRACT
Dacryodes talamancensis D. Santam. & Aguilar, **sp. nov.**, from montane forests of the Cordillera de Talamanca in Costa Rica, is described and illustrated. This is the second species of *Dacryodes* for Central America.

Dacryodes Vahl (Burseraceae) es un género de pequeños o grandes árboles, con flores trímeras, los pétalos usualmente separados, el ovario 2 o 3-locular y los frutos indehiscentes, con el mesocarpo aceitoso y el pireno cartilaginoso y liso (Daly et al. 2011). El género consiste de apróximadamente 90 especies, que se distribuyen en los bosques tropicales de África, Asia y América. En el Neotrópico, cuenta con alrededor de 40 especies, con un centro de diversidad en Colombia (28 especies, además nueve especies adicionales sin describir) (Daly et al. 2011; Daly & Martínez-Habibe 2016).

En América Central solo se encuentran dos especies: *D. patrona* Daly, recientemente descrita de los bosques húmedos en la provincia de Colón, Panamá (Daly 2014); y la especie aquí descrita, de los bosques montanos o premontanos de la Cordillera de Talamanca en Costa Rica. Esta especie aquí descrita representa el primer registro de este género para América Central, el cual fue recolectado en 1992 en la localidad de Alto Lari, Prov. Limón (*Aguilar & Schmidt 1066*). De este remoto e interesante lugar, en la vertiente Caribe de la Cordillera, provienen un sinnúmero importante de novedades para la flora del país. Entre algunos, sobresalen: *Macoubea mesoamericana* J. F. Morales (Apocynaceae), y *Nyssa talamancana* Hammel & Zamora (Nyssaceae), como nuevos registros genéricos para la flora del país; registros de especies conocidas de países vecinos (p. ej., *Blakea arboricola* (Almeda) Penneys & Almeda, *Meriania panamensis* Gleason, Melastomataceae; *Styrax steyermarkii* P. W. Fritsch, Styracaceae); y numerosas nuevas especies (p. ej. *Columnea lariensis* Kriebel, Gesneriaceae; *Guatteria pachycarpa* N. Zamora & Maas, Annonaceae; *Ocotea rufescens* van der Werff, Lauraceae). Para más información sobre esta región y novedades en la flora, ver Grayum et al. (2004), y Zamora et al. (2004a, 2004b). En preparación del tratamiento de Burseraceae para el volumen venidero del *Manual de Plantas de Costa Rica*, se descubrió esta nueva especie, la cual es descrita a continuación.

DACRYODES TALAMANCENSIS D. Santam. & Aguilar, **sp. nov.** TIPO: **COSTA RICA. Puntarenas.** Cantón de Coto Brus, La Libertad de Gutiérrez Braun, orilla del camino, en potrero, 08°55'02" N, 082°54'07" W, 1100 m, 5 Oct 2000 (fls. pistiladas), *E. Alfaro 3458* (holotipo: MO-2 cartulinas, 6726475, 6726476). Figuras 1–3.

Most closely resembling *Dacryodes peruviana* (Loes.) H.J. Lam by the sparsely lenticellate branches, large leaves with acuminate leaflets, and fruits more or less similar in size but distinguished by leaves with (8–) 9–13 leaflets (vs. 7–9), short inflorescenses (9–11.2 cm long, vs. [1.8–] 5–22.5 [27.5] cm), calyx usually truncate (vs. lobed), and petals erect at anthesis (vs. reflexed).

Árbol, 15–45 m × 18–90 cm; **tronco** cilíndrico; **corteza** externa del tronco descrita como blanquecina o gris, exfoliante, la corteza interna con secreción resinosa transparente o blanca (cuando se seca), aromática, pegajosa; ramitas 0.5–1 cm de grueso, teretes, diminutamente pubescentes con tricomas café claro, lenticeladas, las lenticelas elípticas, blanquecinas. **Hojas** imparipinnadamente o (rara vez) paripinnadamente compuestas, distribuidas ± a lo largo de las ramas, 20–43.5 cm de largo, con (8) 9–13 folíolos; **pecíolo** 4.2–11 × 0.3–0.4 cm, diminutamente pubescente o casi glabro, levemente engrosado en la base, no abrazando la rama, usualmente semiterete, esparcidamente lenticelado abaxialmente; **raquis** 9.3–27 × 0.25–3 cm, similar en la pubescencia al pecíolo, estriado, de forma irregular o más o menos triangular, con pequeñas lenticelas blanquecinas sobre ambas superficies; **pecíolulos laterales** 0.4–1.2 cm de largo, rugosos, levemente retorcidos, con dos ligeros surcos adaxialmente, escasamente pubescentes, aparentemente no pulvinados; **pecíolulo terminal** 1.7–3.5 cm, liso, algunas veces con lenticelas, terete o (algunas veces) lateralmente compreso, escasamente pubescente a glabrescente, aparentemente pulvinado distalmente, el pulvínulo rugoso; **folíolos** secando café claro en el haz y verde oliva (con pequeños puntos rojizos o cafezuscos) en el envés, acuminados a abruptamente acuminados en el ápice (con el acumen 0.5–1 cm de largo), enteros, planos, la venación secundaria eucamptódroma, con 10–15 venas laterales por lado irregularmente espaciados y levemente arqueados y (a veces) con nervios intersecundarios, los nervios de orden superior reticulados, todas las venas prominentes en ambos lados, glabros o con tricomas muy esparcidos y pequeños (especialmente a lo largo de la vena media) en ambas superficies, los basales 4.3–10.4 × 3.5–5.7 cm, ovados a lanceolado-elípticos, los laterales (no basales) 8.4–17.8 × 3.2–7.8 cm, elípticos a lanceolados, usualmente asimétricos en la base en un lado y atenuados o redondeados en el otro, el terminal 6.6–13.2 × 3.6–6.5 cm, elíptico a lanceolado, cuneado en la base. **Inflorescencias** 9–11.2 cm de largo, las ramas laterales ca. 2.3 cm de largo, los ejes pubescentes con tricomas café claro y (algunas veces) con cristales blanquecinos, estriados, levemente aplanados, esparcidamente lenticelados, las lenticelas muy destacadas en muestras con frutos; bráctea en el primer eje 2.3–3 mm de largo, estás en el segundo eje 1.2–1.3 mm de largo, deltadas a angostamente deltadas o lanceoladas, densamente pubescentes abaxialmente, agudas en el ápice; bracteolas 0.6–0.8 mm de largo, angostamente deltadas, agudas en el ápice, densamente pubescentes abaxialmente, glabras adaxialmente. **Flores estaminadas** desconocidas. **Flores pistiladas** con pedicelo 1–2.7 × 0.6–0.8 mm, más o menos rectangular-compreso, pubescente (en fr. 6–9 × 1.1–2.1 mm, terete a rectangular-compreso, estriado y cortamente pubescente); **cáliz** 1–1.3 × 2–3 mm, cupular, truncado o (rara vez) levemente lobulado, pubescente abaxialmente y (algunas veces) con cristales blanquecinos, glabro adaxialmente; **pétalos** 3–3.1 × 1.3–2 mm, crema, erectos en la antesis, separados, ampliamente ovados, levemente revolutos, adpreso-pubescentes abaxialmente (especialmente hacía el ápice) y algunas veces con cristales blanquecinos, glabros adaxialmente, no papilados en el margen, apiculados en el ápice (con el apiculo ca. 0.1 mm) o (algunas veces) redondeados; **estaminodios** 6, insertos afuera en la base del disco, ca. 1 mm de largo, las anteras continuas con el filamento, ca. 0.5 mm de largo, deltado-redondeadas, glabras; **disco** ca. 0.5 mm de alto, carnoso, lobulado, glabro; **pistilo** ca. 2 × 1.5 mm, glabro, el ovario bilocular, ovoide; **estilo** ca. 0.3 mm de largo; **estigma** 0.6–0.8 mm de ancho, capitado a discoide, papilado. **Frutos** verdes, 1.6–2.4 × 1–2.2 cm, indehiscentes, rugosos cuando secos o (rara vez) lisos (*E. Alfaro 3458*), ovoides (cuando jóvenes), ovoides a globosos, obtusos o acuminadso en el ápice, glabros o con escasa y diminuta pubescencia.
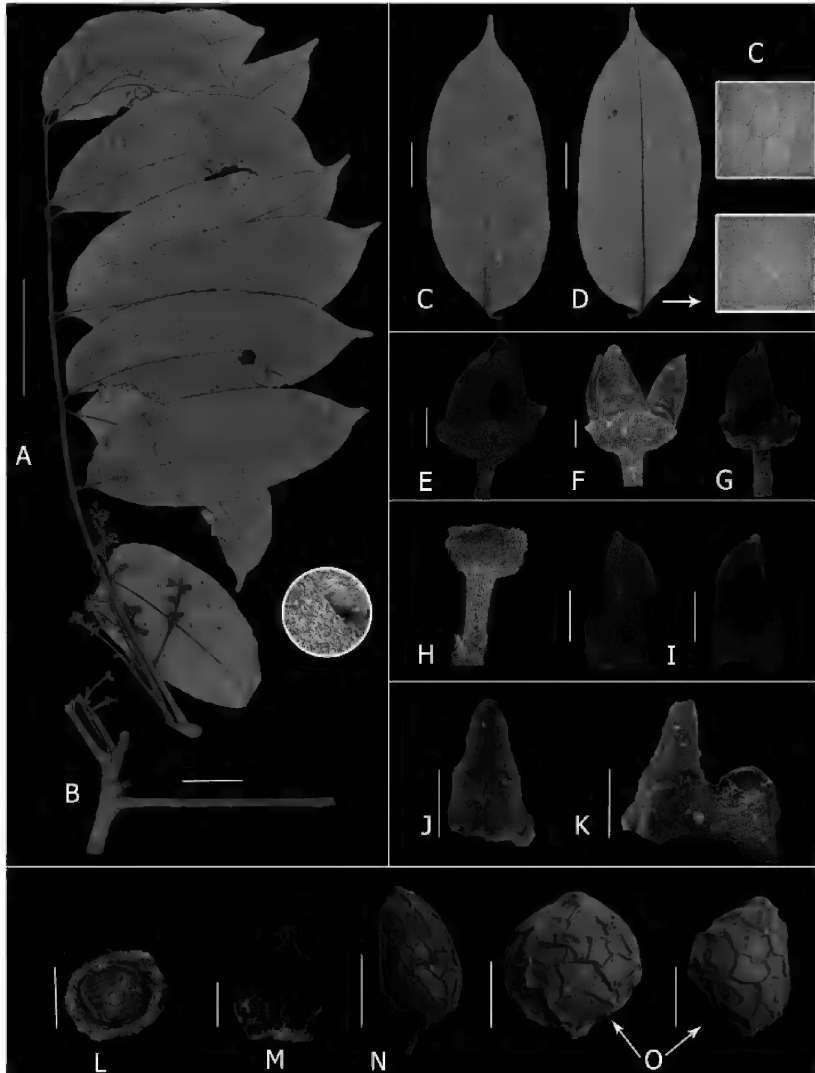
Figura 1. *Dacryodes talamancensis*. A. Rama con inflorescencia, en círculo detalle del indumento en los ejes de la inflorescencia (barra=5 cm). B. Ramita y pecíolo (barra=2 cm). C. Folíolo y detalle de la venación por el haz (barra = 2 cm). D. Folíolo y detalle de la venación por el envés (barra=2 cm). E. Botón floral (barra=5 mm). F. Flor mostrando los tres pétalos (barra=5 mm). G. Flor con los dos pétalos removidos, mostrando el disco, pistilo y estaminodios. H. Cáliz e indumento. I. Pétalo mostrando ambos lados (barra=5 mm). J. Estaminodio (barra=5 mm). K. Estaminodio y parte del disco (barra=5 mm). L. Vista desde arriba del disco (barra=1 mm). M. Ovario (barra=5 mm). N. Fruto inmaduro (barra=1 cm). O. Fruto maduro, visto de frente (izquierda) y vista lateral (derecha) (barra=1 cm). A–M de *Alfaro 3458* (MO); N de *Zamora 2694* (MO) y O de *Zamora 2982* (MO).

Fenología. Flores pistiladas han sido recolectadas en octubre; frutos en febrero y marzo.

Etimología.   El epíteto específico, *talamancensis,* hace referencia a la Cordillera de Talamanca, localidad de donde provienen todas las colecciones.

Hábitat y distribución.   *Dacryodes talamancensis* se conoce de ambas vertientes de la Cordillera de Talamanca en Costa Rica. En la región de Alto Lari (vertiente Caribe), crece a los 450 m de elevación, mientras que en la región de San Vito de Coto Brus (vertiente del Pacífico), crece entre los 1100 y 1118 m de elevación. También ha sido observada por el río Chirripó (Duchí), a ca. 550–600 m de elevación (Prov. Limón) (M. H. Grayum 2016, comun. pers.), y en territorio panameño en los alrededores de cerro Frío y río Tskui, vertiente Caribe (Prov. de Bocas del Toro); lástimosamente, no fueron documentadas por una muestra de herbario para poder corroborar dicha deducción.
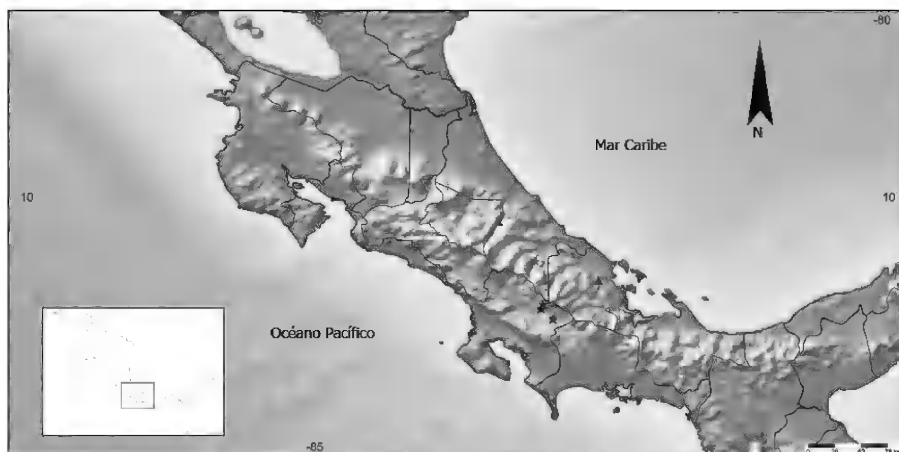

Figura 2. Mapa de distribución de *Dacryodes talamancensis* (★) y localidad donde fue observada en territorio costarricense y panameño (▲).

Dacryodes talamancensis se reconoce por sus hojas con 9–13 folíolos que llegan a tener una coloración café claro en el haz y verde oliva (con puntos rojizos o cafezuscos) en el envés cuando secos, casi glabros sobre ambas caras y con los nervios conspicuos sobre ambos lados; flores con el cáliz cupular y usualmente truncado, los pétalos separados, adpreso-pubescentes abaxialmente, sin papilas en el margen, el ovario glabro y el estigma capitado a discoide; y sus frutos ovoides a globosos y usualmente rugosos cuando secos. También se destaca por sus ramitas, pecíolos y ejes de la inflorescencia lenticelados, sus hojas con el raquis lenticelado y de forma irregular o más o menos triangular y sus inflorescencias, cálices y pétalos con cristales blanquecinos. Esta especie también es un árbol de gran tamaño, con la corteza externa blanquecina o gris, exfoliante, con resina arómatica, transparente a blanca, y crece en hábitats montanos o premontanos. La ilustración y texto bajo "*Dacryodes* sp." en Zamora V. et al. (2000: 42) corresponden a esta nueva especie.

Dacryodes talamancensis se puede diferenciar de la panameña *D. patrona* (Prov. Colón, 100–130 m de elevación), ya que esta última tiene hojas con el pecíolo más corto (1.7–5.1 cm, vs. 4.2–11 cm de largo) y menos folíolos (3–5, vs. 9–13) sin puntos en el envés (vs. con puntos rojizos o cafezuscos) y frutos más pequeños (1.6–1.8 × 1.1–1.3 cm, vs. 1.6–2.4 × 1–2.2 cm). Aunque de *D. patrona* solamente se conocen las inflorescencias y flores estaminadas y en *D. talamancensis* las

pistiladas, en la primera especie las inflorescencias son más cortas (7.5 cm largo, vs. 9–11.2 cm) y sobre ejes no muy robustos (vs. robustos) y las flores tienen el cáliz 0.5–0.6 × 1.6–1.8 mm (vs. 1–1.3 × 2–3 mm) y los márgenes de los pétalos papilados (vs. sin papilas).

Figura 3. *Dacryodes talamancensis.* A. Rama con hojas, mostrando el envés de los folíolos. B. Rama con hojas, mostrando el haz de los folíolos. C. Envés de los folíolos. Fotos por A.K. Monro, de *Santamaría & Monro 8771.*

En Costa Rica, otras especies de Burseraceae con flores trímeras son *Bursera standleyana* L. O. Williams & Cuatrec. y *Trattinnickia aspera* (Standl.) Swart. La primera sobresale por su extraño hábito epifítico o hemiepifítico, con la corteza roja o rojiza a morado rojizo o café rojizo a café, mientras que la segunda tiene folíolos ásperos en ambas superficies, flores con los pétalos parcialmente connatos y pirenos gruesos y rugosos. Además de las mencionadas arriba, *Bursera ovalifolia* (Schltdl.) Engl., es otra especie con flores trímeras (al menos las pistiladas), pero tiene corteza exfoliante rojiza y hojas usualmente trifolioladas.

Las medidas de las inflorescencias pistiladas presentadas en la diagnosis proviene de Daly & Martínez-Habibe (2016: 125).

Especímenes adicionales examinados. COSTA RICA. Limón: Talamanca, Bratsi, Alto Lari, siguiendo la fila entre río Dapari y río Lari, bajando hasta el cauce del mismo, 09°25'50"N, 083°03'20"W, 450 m, 03 Mar 1992 (est., pero la etiqueta describe frs. recolectados "del suelo"), *Aguilar & Schmidt 1066* (CR [ex-INB]). **Puntarenas:** Buenos Aires, cuenca del Térraba-Sierpe, Altamira, finca de ASOPROLA, 09°00'31"N, 083°00'21"W, 1100 m, 22 Feb 2006 (est.), *González et al. 420* (CR [ex-INB]); Parque Internacional La Amistad, sector Casa Coca, Punto 08, 09°02'57"N, 082°59'20"W, 1950 m, 03 Abr 2011 (estéril), *Santamaría & Monro 8771* (CR, imagen digital); Coto Brus, Pittier, bajo de Palmira, orillas del camino a Palmira, 08°55'25"N, 082°54'07"W, 1100 m, 24

Abr 1998 (fr), *Zamora et al. 2694* (MO-2 sheets); San Vito de Coto Brus, La Libertad camino a Palmira, 08°54'49"N, 082°54'02"W, 25 Feb 2000 (fr), *Zamora & Aguilar 2982* (MO-2 cartulinas).

AGRADECIMIENTOS

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LECTOTYPIFICATION AND SYNONYMY OF *CASTILLEJA ARVENSIS* (OROBANCHACEAE), WITH NOTES ON ITS STATUS, IDENTIFICATION, AND RELATIONSHIPS

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ABSTRACT

A lectotype is designated for *Castilleja arvensis* Schltdl. & Cham. and a full synonymy is provided. A lectotype is also designated for the synonymous name, *Castilleja haitiensis* Urb. & Ekm. The annual *C. arvensis* is also distinguished from the designated lectotype of the perennial species *C. lithospermoides* Kunth (a nomenclatural synonym of *C. scorzonerifolia* Kunth) and from other species with which *C. arvensis* is often confused. A simplified key and vouchered field photograph are provided for distinguishing *C. arvensis* from its morphologically similar congeners.

Castilleja arvensis Schltdl. & Cham. is an annual found throughout much of Mexico, Central America, and South America, from near sea level to above timberline, largely in ruderal habitats such as roadsides, grazed and agricultural lands, and forest edges and also in lower paramos, volcanic debris fields, and other moderately natural habitats. It has spread to island groups, including the Galapagos and the Hawaiian and Caribbean archipelagos; it has yet to be documented north of the Mexican border in North America.

In the protologue (Schlechtendal & Chamisso, 1830) for *Castilleja arvensis* two herbarium sheets collected by C.J.W. Schiede and F. Deppe in the vicinity of the city now known as Xalapa, Veracruz, Mexico, were cited. The protologue lists the locations as "Parce prope Jalapam, inter segetes inter San Andres et Serro colorado." The two collections are of the same species and bear the same Schiede number and date (August 1828), and are labeled as "Typus." Locations recorded on the two sheets are different, indicating that they were perhaps collected in different localities and necessitating the designation of a lectotype. Holmgren (1978), in his treatment of the *Castilleja* species of Costa Rica and Panama, cited both collections as "Type." He also mentioned "Type not seen," and he may have not realized two syntype sheets were involved. One syntype sheet, HAL 096090, is labeled "inter segetes inter San Andres et Serro Colorado;" the other is selected as the lectotype designated below.

CASTILLEJA ARVENSIS Schltdl. & Cham., Linnaea 5: 103. 1830. **LECTOTYPE** (designated here): **MÉXICO**. [**Veracruz**]: Parce prope Jalapam [= Xalapa] (prope Jalapam parce provenit), Aug 1828, *C.J.W. Schiede 542 and F. Deppe* (HAL 096089!). Figure 1. [Note: The collections cited by Schlechtendal and Chamisso in the Linnaea paper are assumed to be collected by both Schiede and Deppe; the latter's name does not appear on either of the syntype sheets at HAL. The lectotype sheet was selected due to the more ample material thereon.]

Bartsia trinervis Ruîz & Páv. ex A. Lopéz, Anal. Inst. Bot. Cavanilles 17: 445. 1959. **TYPE**: **SOUTH AMERICA**. Ic. 496, fig. b. [no collection data provided] (holotype: MA?).

Castilleja agrestis Pennell, Fieldiana Bot. 28: 519. 1953. **TYPE**: **MEXICO**. **Michoacan**. Cornfields near Patzcuaro, 18 Nov 1890, *C.G. Pringle 3349* (holotype: PH!; isotypes: BR!, E!, S!).

Castilleja communis Benth., in DC., Prodr. Syst. Nat. Regn. Veg. 10: 529, 1846. LECTOTYPE
(Holmgren, Brittonia 30: 185, 1978): México. Veracruz. Jalapa [= Xalapa], (Apr 1838) *J.J. Linden 212* (lectotype: K!; isolectotypes: BR-GENT!, G!, MICH!). [Note: Holmgren (1979) stated that F.W. Pennell made the original lectotypification for this taxon, using *Linden 212* but made no mention of the published source of Pennell's lectotypification. I have been unable to find any such reference by Pennell for this study, and I believe Holmgren's citation was based on Pennell's unsigned annotation of *Linden 212* as "Type specimen" on the type sheet at K. This sheet contains two other collections besides *Linden 212*. A year earlier, Holmgren (1978) cited *Linden 212* as the "Type" for *C. communis*, and I am taking this to be the effective lectotypification, pending discovery of an earlier publication by Pennell. Some unpublished sources cite the location of Pennell's putative lectotypification as his paper on the Scrophulariaceae of Panama (Pennell 1940); I find no such lectotypification in that publication.]

Castilleja communis Benth. f. *johnstoniae* Standl., Field. Mus. Pub. Bot. 23: 86. 1944. TYPE:
Guatemala. Dept. Escuintla: between Río Jute and Río Pantaleón, on road between Escuintla and Santa Lucía Cotz. [= Santa Lucía Cotzumalguapa], in moist (damp) field, (alt. 540-720 m), 24 Jan 1939, *P.C. Standley 63500* (holotype: F!). [Note: This was described as a pale color form. Such rare color forms occur rarely and sporadically throughout the range of this normally reddish-bracted species.]

Castilleja haitiensis Urb. & Ekm., Arkiv. Bot. 23A, 11: 46. 1931. LECTOTYPE (designated here):
Haiti. Massif de la Hotte, in parte occidentali prope Torbec inter Les Platons et Farmon in campis, 1000 m alt., 26 Dec 1926, *E.L. Ekman 7421* (lectotype: S 04-3441!; isolectotypes: A!, C!, F!, G! GH[2]!, K!, NY!, S 04-3440!, TEX-LL!, US!). [Note: two sheets with identical labels and both annotated as "Typus" are found at S. The sheet selected as lectotype contains Ekman's field notes, perhaps indicating that this was his intended holotype.]

Castilleja hyssopifolia G. Don, Gen. Syst. Gard. Bot. 4: 615. 1838. TYPE: **Ecuador**. "*Willd. Herb #11697*", [*Humboldt 2294*, from vicinity of Quito, 1802] (holotype: B-WILLD!). [Note: Don's intention in listing this name is not entirely clear. It is included in a numbered paragraph under the species *Castilleja lithospermoides* Kunth, listed as "*C. hyssopifolia,* Willd. Herb. No. 11697," and was likely intended as a nomen subnudum to be included within the synonymy of *C. lithospermoides*. Don provided a partial description of the plant, possibly contrasting it with *C. lithospermoides*, though there is no clear designation of the collection as a "typus." This collection is conspecific with the type of *C. arvensis* and not with lectotype of *C. lithospermoides* from Mexico.]

Castilleja lithospermoides Kunth var. *pastorei* Hicken, Physis. Revista de la Sociedad Argentina de
Ciencias Naturales 1: 30. 1912. TYPE: **Argentina**. En el Cerro del Ruidito (San Luis), 20 Jan 1911, *F. Pastore s.n.* (holotype: SI!).

Castilleja pulcherrima Sessé & Moç., Icones Fl. Mex., plate 104. 1889; Pl. Nov. Hisp., Ed. 1: 95.
1889 (La Naturaleza, Ser. II.i., App. 95). LECTOTYPE (Nelson**,** Anales Jard. Bot. Madrid 55: 375-418. 1997): **México**. [**probably Distrito Federal**]. In agris Sancti Angustini [= San Agustin de las Cuevas, = Tlalpan] oppido prope Mexicum, Sep [1787 or 1788], *M. Sessé 2523* (lectotype: MA!; photograph: F!, negative #30810. [Note: The lectotype cited by Nelson (1997) bears the annotation, "*Castilleja pulcherrima* N." (= Nova). A discussion of this name was provided by McVaugh (2000).]

Discussion

Castilleja arvensis is at times confused with several related species of *Castilleja* sect. *Euchroma* (Nutt.) Benth. This is true on herbarium sheets as well as in some publications (e.g. Xifreda 1999; Páez et al. 2015). This is true because of morphological similarities and misinterpretations of the identity of *C. lithospermoides* Kunth. This misinterpretation has led some authors (e.g., Xifreda 1999) to synonymize *C. arvensis* under the earlier-described *C.*

lithospermoides. My studies of the type material involved and the literature concerning the *Castilleja* species of Mexico and my own field studies of *Castilleja* in Mexico, Central America, and South America lead to a different conclusion.

The first relevant consideration is the identity of *Castilleja lithospermoides* Kunth. In his protologue (Nov. Gen et Spec. 2 [folio]: 266, 1818; 2 [quarto]: 331, tab. 164, 1920), Kunth listed two collections: "Crescit in temperatis Novae Hispaniae prope Real del Monte et Moran, et in Regno Quitensi prope Chillo." The former is a historically famous mining district (including Real del Monte and Real del Moran) in the mountains northeast of Pachuca, Hidalgo, Mexico; the latter is near Quito, Ecuador. In her comprehensive revision of the *Castilleja* species of Mexico, Eastwood (1909) not only treated *C. lithospermoides* as distinct from *C. arvensis* but also provided an effective lectotypification of the former, based on the collection from Mexico: "The type was collected probably in the state of Hidalgo near Real del Monte." This is surely synonymous with the "Novae Hispaniae prope Real del Monte et Moran" of the protologue, and no other type material applying to *C. lithospermoides* is known to me. Of the type material associated with the name *C. lithospermoides* at P, there are two sheets –– one usually is regarded as the type (Nesom 1992) and as Eastwood's lectotype (Figure 2, P00670473), and the other is labeled as isotype, though it is best regarded as an isolectotype (Figure 3, P00136105, perhaps an addition from Bonpland's personal herbarium, based on the annotations). Both sheets are labeled with the collection location as "Moran," though it is not clear if all stems were collected at that location. Both sheets contain three stems. Of these, only one stem on the type sheet but all three on the isotype sheet contain complete inflorescences, and all of these four stems have corollas partially exserted from the calyces. Only the stem on the right side of the type sheet contains roots to indicate duration. That stem lacks an inflorescence. The central stem on the type sheet has neither root nor a complete inflorescence, the latter apparently due to past insect damge, and is of little determinative value, though the linear-lanceolate leaves are consistent with those of the left stem and not with *C. arvensis*. The stem with the root is divergent from the others in its nodulose proximal portion and may actually represent the specimen from near Quito cited in the protologue. It belongs to what is here interpreted as *C. arvensis*, though its collection location is conjectural, and *C. arvensis* is found both in Mexico and in Ecuador. What is certain is the left stem on the type sheet (the only one with an inflorescence), likely the middle stem, and all the stems on the isolectotype sheet are distinct from the type of *C. arvensis*. In addition, both the tab. 164 illustration (Figure 4) and the written description of *C. lithospermoides* show features not found in *C. arvensis*, including a reddish band on the distal portion of the calyces and the clearly exserted distal portion of the corolla. Eastwood's key also correctly identifies *C. arvensis* as an annual, contrasting it with the perennial *C. lithospermoides*. Finally, on the type sheet of the *C. arvensis* synonym, *C. communis* Benth., Bentham in an undated annotation observed that "All these (the three collections on the sheet) belong to a species common in South America, which I took for *C. lithospermoides* Kunth, but now I think it is an undescribed one." Evidently, Bentham was not aware at the time of the publication of *C. arvensis*.

Another important point to consider in relation to these plants is the close similarity between *Castilleja lithospermoides* and *C. scorzonerifolia* Kunth, both in their type specimens and in the illustrations accompanying the protologues. This was noted by Nesom (1992a) when he reduced *C. lithospermoides* to synonymy under *C. scorzonerifolia*. This conclusion was evidently also supported by *Castilleja* researcher T.I. Chuang, who annotated the isolectotype sheet of *C. lithospermoides* as *C. scorzonerifolia*. Finally, the perennial *C. scorzonerifolia*, including *C. lithospermoides*, is limited to the eastern and southern portions of Mexico, where it is endemic; the annual *C. arvensis* has a much wider range, including much of Mexico, Central America, and South America. Most, if not all, material in herbaria identified as *C. lithospermoides* and collected outside of Mexico is likely referable to *C. arvensis*.

Yet another species to consider in this discussion is *Castilleja nervata* Eastw. It is found primarily in the Sierra Madre Occidental and Sierra Madre del Sur of Mexico and scarcely enters the USA in the Chiricahua and possibly the Santa Rita Mountains of Cochise Co., Arizona. Like *C. arvensis*, *C. nervata* has a corolla mostly included within the calyx and lacks the brightly-colored distal portion of the calyces; unlike that species, *C. nervata* is perennial and also differs from *C. arvensis* in leaf morphology and seed characteristics. Despite these differences, the identification of these two species is often confused in herbarium specimens collected from the western and southern mountains of Mexico.

The following key can be used to distinguish the species discussed here and should help with the proper identification of these plants both in the field and herbarium. Several other species of sect. *Euchroma* occur in Mexico (see Nesom 1992b); they are all rare to uncommon and highly range-restricted endemics, most of which would separate out with *Castilleja scorzonerifolia* in the first couplet. Vouchered field photographs of all three species treated in the key are also provided below (Figures 5-14). Additional photographs of the genus *Castilleja* from throughout its range, including all species of sect. *Euchroma*, can be found at my Flickr site (Egger 2017).

1. Calyces proximally greenish, distally brightly and contrastingly colored red to orange or red-orange (yellow, rich purple); distal portion of corolla shortly, conspicuously exserted from calyces ……………………………….. **Castilleja scorzonerifolia** and other species of sect. *Euchroma* in Mexico
1. Calyces usually greenish throughout, distally greenish to dark greenish to sometimes dull, dark purplish in *C. nervata*; corollas usually wholly included within the calyces or sometimes slightly, inconspicuously exserted.

    2. Plants annual; seeds linear, 400–500 per capsule, 0.8–1.0 mm long, 0.1–0.2 mm wide; leaves usually oblanceolate to lanceolate, often broadly so; stems usually proximally nodulose ……………………………………………………………………………………… **Castilleja arvensis**
    2. Plants perennial; seeds narrowly ovate, 50–150 per capsule, 1.3–3.0 mm long, 0.5–1.1 mm wide; leaves usually linear-lanceolate; stems proximally more or less smooth .... **Castilleja nervata**

ACKNOWLEDGEMENTS

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Figure 1. Lectotype of *Castilleja arvensis* Schltdl. & Cham., HAL.

Figure 2. Eastwood's lectotype of *Castilleja lithospermoides* Kunth, P.

Figure 3. Isolectotype of *Castilleja lithospermoides* Kunth, P.

Figure 4. Painted version of Tab. 164, *Castilleja lithospermoides* Kunth.

Figure 5. *Castilleja arvensis*, Pasachoa Forest Reserve, Pichincha Prov., Ecuador, 13 Jul 1987. Two stems from same population showing variation in leaf morphology in this species.

Figure 6. *Castilleja arvensis* as an adventive on the Island of Hawaii. (L) Kipuka P'uu O'o, 14 Jul 1999. (R) Color variations, near Hilo Airport, 1 Aug 1997.

Figure 7. *Castilleja arvensis*, variation in size and habitat. (L) Plant about 25 cm tall on volcanic cinders, Kipuka P'uu O'o, Island of Hawaii, 14 Jul 1999. (R) Plant nearly 1.5 m tall supported by fence, cloud forest margins, Lower Chiriboga Rd., Pichincha Prov., Ecuador, 9 Jul 1987.

Figure 8. *Castilleja arvensis* variation. (L) Above Santa Inez del Monte, Sierra Clavellinas, Oaxaca, Mexico, 22 Aug 2001. (R) East of Agallpampa, Depto. La Libertad, Peru, 16 Apr 2005.

Figure 9. *Castilleja scorzonerifolia* (syn: *C. lithospermoides*), typical plants. (L) NE slopes of Cerro Potosí, Nuevo León, Mexico, 1 Aug 1999. (R) Near Tlachichuca, Puebla, Mexico, 19 Aug 2000.

Figure 10. *Castilleja scorzonerifolia*, high elevation forms, upper slopes of Cerro Zempoalteptl, Oaxaca, Mexico, 24 Aug 2001.

Figure 11. *Castilleja scorzonerifolia*, unusual color forms. (R) Near Tlachichuca, Puebla, Mexico, 19 Aug 2000. (L) NE slopes of Cerro Potosí, Nuevo León, Mexico, 1 Aug 1999.

Figure 12. *Castilleja nervata*, N of Turkey Cr., Chiricahua Mts., Cochise Co., Arizona, 20 Aug 1992.

Figure 13. *Castilleja nervata*. (L) N of Turkey Cr., Chiricahua Mts., Cochise Co., Arizona, 20 Aug 1992. (R) near Laguna Zempoala, Estado de Mexico, Mexico, 22 Aug 2000.

Figure 14. *Castilleja nervata*, form with unusually colored calyces, near El Palmito, Sierra Madre Occidental, Sinaloa, Mexico, 13 Apr 1999.

All field photographs are by the author and most are vouchered with the following collections deposited at WTU, with some duplicates deposited at MEXU, CAS, NY, and elsewhere.

Castilleja arvensis

Fig. 5: no collection obtained.

Fig. 6: (L): Egger 1076
      (R): Egger 895

Fig. 7: (L): Egger 1076
      (R): no collection

Fig. 8: (L): Egger 1185
      (R): Egger 1330

Castilleja scorzonerifolia

Fig. 9: (L): Egger 1087
      (R): Egger 1126

Fig. 10: (L): Egger 1196
      (R): Egger 1197

Fig. 11: (L): Egger 1126b
      (R): Egger 1087

Castilleja nervata

Fig. 12: Egger 529

Fig. 13: (L): Egger 529
      (R): Egger 1138

Fig. 14: Egger 1059

A COLLECTION OF *SOLIDAGO RUPESTRIS* (ASTERACEAE: ASTEREAE) FROM MINERAL CO., WEST VIRGINIA

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ABSTRACT
A collection of *Solidago rupestris* first thought to be from western Maryland and mapped for that state was determined to be from adjacent Mineral Co., West Virginia. This is the first collection from West Virginia seen by the authors.

Solidago rupestris Raf. (Asteraceae: Astereae) was listed as occurring in Indiana, Kentucky, Maryland, Pennsylvania, Tennessee, and Virginia in Flora North America (Semple & Cook 2006). A collection borrowed from NY (Thiers continuously updated) and examined as part of the first author's research on the genus has an N.Y.B.G. herbarium label with a hand-written identification to species and the following location and collector information in cursive script: "Cumberland. Md. Devil Slide, Howard Schriver [sic] s.n. 1894" –– it is most likely a collection made by Howard Shriver. Cumberland is in Allegany Co., Maryland, just north of the Potomac River, and this was the location mapped for the distribution range map posted online by Semple (2016 frequently updated).

In January 2017 when the second author requested location information to update distributions in the Rare, Threatened, and Endangered Plants of Maryland (Maryland Natural Heritage Program 2016), data on three Maryland locations were sent and an email exchange followed regarding the *Shriver s.n.* collection that included a correction to the collector name, which had been transcribed incorrectly. Subsequently, it was discovered in a Google search that Devil's Slide was located on the south side of the river, which put the collection in Mineral Co., West Virginia, according to the 21 April 1893 Railroad Gazette report (vol. 25, p. 309), on railroad construction about 1 mile south of Cumberland. Howard Shriver (1824-1901), a local school teacher with a keen interest in botany, collected extensively in the vicinity of Cumberland in the 1890s but the location information on specimens that were frequently stamped "near Cumberland" is vague about which state. This particular collection was from the West Virginia side of the river although the label has "Md." Correct data for the Shriver collection are **West Virginia**. Mineral Co.: Cumberland, Devil's Slide, 1894, *Howard Shriver s.n.* (NY; Fig. 1).

Figure 1. *Solidago rupestris* from Devil's Slide, Mineral Co., West Virginia: *H. Schriver s.n.* (NY).

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UNA NUEVA ESPECIE DE *CASTILLEJA* (OROBANCHACEAE) DEL CENTRO DE MÉXICO

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RESUMEN

Se propone como nueva y se ilustra a **Castilleja madrigalii** C. Medina & E. Carranza, **sp. nov.**, que crece en un área reducida del noreste del estado de Guanajuato, México, perteneciente a la Sierra Madre Oriental. La planta se ubica en la secc. *Euchroma* y es semejante a *C. scorzonerifolia*, de la que difiere mayormente en sus bráceas amarillas (no rojas o moradas), así como a *C. hidalgensis*, que es de notablemente menor tamaño y tiene flores con el estigma más profundamente lobado.

ABSTRACT

Castilleja madrigalii C. Medina & E. Carranza, **sp. nov.** is proposed and illustrated. It grows in a small area of the northeastern part of the Mexican state of Guanajuato, in the Sierra Madre Oriental mountain range. It belongs to sect. *Euchroma* and is similar to *C. scorzonerifolia*, from which it differs in its yellow (not red or purple) bracts, as well as to *C. hidalgensis*, a notably smaller plant bearing flowers with a more deeply lobed stigma.

Como resultado de las exploraciones llevadas a cabo para dar cumplimiento al proyecto Flora del Bajío y de Regiones Adyacentes, se ha colectado buena cantidad de especímenes botánicos e información medioambiental, de una basta área del centro de México. Entre este material se encontraron algunos ejemplares del género *Castilleja* Mutis ex L.f. (Orobanchaceae, antes Scrophulariaceae), pertenecientes a una entidad que aún no ha sido descrita y que aquí se presenta.

Las especies mexicanas de este género han sido revisadas por Eastwood (1909) y posteriormente varios autores han contribuido a su mayor conocimiento; entre los más recientes cabe mencionar a Holmgren, 1976; Nesom, 1992a, 1992b, 1992c, 1992d, 1992e, 1994; Egger, 2002a, 2002b, 2017; Iltis et al. 2003; Francisco-Gutiérrez, 2014; Francisco-Gutiérrez et al. 2016.

A continuación se propone como especie nueva a:

CASTILLEJA MADRIGALII C. Medina & E. Carranza, **sp. nov. Tipo: MÉXICO. Guanajuato**. Municipio de Xichú: ca. 6 km de El Huamúchil, por la carretera a Agua Zarca de Romerillos, 1 Oct 2009, *E. Pérez-Calix 5043* (holotipo: IEB). Figura 1.

Herba perennis decumbens vel erecta caulibus 15–50 cm longis dense puberulis et cum pilis longioribus sparsioribus tectis; folia plerumque lanceolata 7–47 mm longa, 2–10 mm lata; inflorescentiae spiciformes (2–)5–16(–30) cm longae bracteis spathulatis vel oblongis (16–)18–22 mm longis luteis vel luteolis; calyx tubulosus 18–22 mm longus bilobatus, lobulis margine integro vel undulato, ad basem viridis, ad apicem luteolus; corolla 20–26 mm longa luteo-viridula labii tridentati membranacei ad petaloidei, galea 6–11 mm longa; stylus 26–32 mm longus stigmate globoso ad leviter bilobato; capsula longe ovoidea apiculata 7–11 mm longa; semina ellipsoidea 1–1.3 mm longa brunnea.
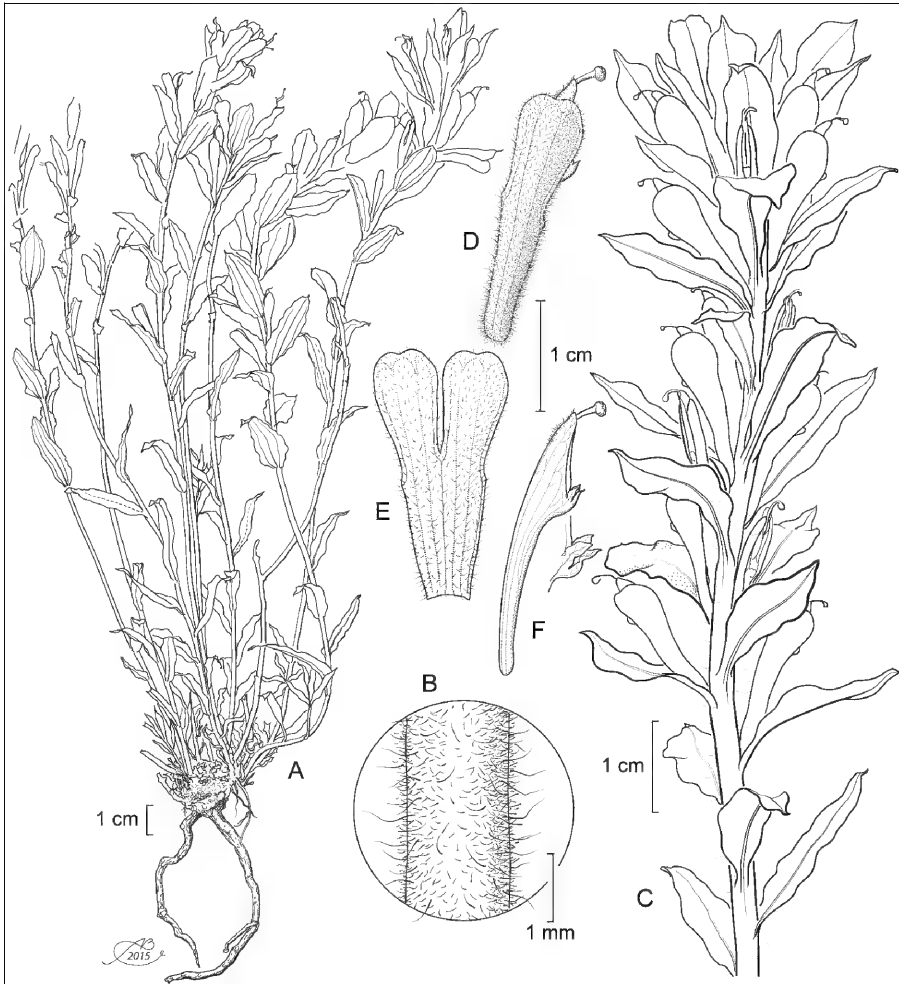
Figura 1. *Castilleja madrigalii.* A. Aspecto general de la planta. B. Detalle de la pubescencia del tallo. C. Parte superior del tallo con inflorescencia. D. Vista lateral del cáliz. E. Cáliz abierto en vista adaxial. F. Vista lateral de la corola y detalle del labio inferior. Basado en *E. Pérez-Cálix 5043*; ilustrado por Alfonso Barbosa.

Hierba perenne, con varios tallos partiendo de la base, decumbentes a erectos, en ocasiones ramificados, de 15–50 cm de largo, densamente pubérulos y además con pelos más largos espaciados, base leñosa; raíces 2(–3) delgadas, casi fibrosas; hojas sésiles, lanceoladas variando a elípticas u oblanceoladas, más o menos sobrepuestas, de 7–47 mm de largo, de 2–10 mm de ancho, base en ocasiones semiamplexicaule, ápice agudo a redondeado, margen entero, a veces ondulado a casi crenulado, lámina con 1–3 nervios inconspicuos en el haz, ± prominentes en el envés, pilosa; inflorescencias en espigas terminales, de (2–)5–16(–30) cm de largo; brácteas espatuladas a oblongas, de (16–)18–22 mm de largo, de (6–)8–12 mm de ancho, amarillas o amarillentas, ápice

agudo a redondeado, en ocasiones algo retuso o más o menos emarginado, margen y venas ciliados, con pelos hasta de 2 mm de largo; cáliz de 18 a 22 mm de largo, tubular, base verde, angosta, ensanchándose hacia el ápice amarillento, densamente pubérulo, sobre todo en la punta, bilobado, la hendidura abaxial de 5–6 mm de largo, la adaxial de 3–3.5 mm de largo, lóbulos con el margen entero o ondulado; corola de 20–26 mm de largo, amarillo-verdosa, mayormente glabra a escasa y finamente pubescente, labio inferior tridentado, membranáceo a petaloide, el diente central aproximadamente de 0.5–1.5 mm de largo, los laterales de alrededor de 1–1.5 mm de largo, gálea de 6–11 mm de largo, amarilla, pubérula; anteras de 1.5–2 mm de largo; estilo de 26–32 mm de largo, ligeramente exerto, estigma capitado a ligeramente bilobado; cápsula largamente ovoidea, apiculada, de color marrón oscuro, de 7 a 11 mm de largo, el pico de ± 2 mm; semillas elipsoideas, de 1–1.3 mm de largo, de color café.

Esta especie se ha encontrado en flor de septiembre a noviembre y en fruto de octubre a diciembre.   El epíteto específico se dedica a Xavier Madrigal-Sánchez, quien ha trabajado incansablemente en la exploración botánica en México durante las últimas cuatro décadas.

Material adicional revisado.   MÉXICO. Guanajuato. Municipio de Atarjea, 29.6 km de Xichú, 7 km de Guamúchil, *E. Pérez–Calix, E. Carranza* y *R. Spellenberg 3900* (IEB); Municipio de Xichú, ca. 8 km de El Guamúchil por la carretera a Agua Zarca de Romerillos, *E. Pérez–Calix 5042* (IEB); Municipio de Xichú, ca. 6 km de Guamúchil por carretera a Agua Zarca, 21°18'23" N, 99°55'20" W, *E. Carranza* y *C. Medina 7804* (IEB).

Este nuevo taxón mexicano se conoce sólo del extremo noreste del estado de Guanajuato, donde crece en pequeñas poblaciones.   Desde el punto de vista fisiográfico, esta zona se localiza en la Sierra Madre Oriental, en algunas estribaciones de la porción conocida como "Sierra Gorda".

Castilleja madrigalii es componente del bosque tropical caducifolio, donde predominan plantas como *Bursera morelensis, B. fagaroides, Acacia coulteri, Lysiloma microphyllum, Cordia boissieri, Morkillia mexicana, Ipomoea rzedowskii,* y *Neopringlea integrifolia.*   Crece entre 1300 y 1450 m de altitud, por lo general en laderas de exposición hacia el sur, sobre suelos delgados o poco profundos, a menudo pedregosos, derivados mayormente de rocas calizas.

Debido a que el cáliz de esta planta está dividido en dos partes casi iguales con los segmentos enteros y redondeados, sus flores se encuentran agrupadas en espigas y sus brácteas son más anchas que las hojas caulinares, *Castilleja madrigalii* se ubica como miembro de la sección *Euchroma* (Nutt.) Benth., de acuerdo con Eastwood (1909).   La especie nueva se asemeja más a *C. scorzonerifolia* Kunth y a *C. hidalgensis* J.M. Egger, pero difiere de la primera en sus brácteas y cáliz amarillos o amarillentos, sus dientes petaloides en el labio inferior de la corola, la pubescencia esparcida del cáliz y en su distribución geográfica y ecológica.   Se parece a *C. hidalgensis* en el color y la forma del cáliz, así como en los dientes petaloides del labio inferior y en el hábitat en que crece, pero difiere en el mayor tamaño del tallo y de la inflorescencia, en el largo menor de los dientes petaloides del labio inferior de la corola y en el estigma menos profundamente lobado.   Por otra parte, mientras *C. madrigalii* y *C. hidalgensis* son endemismos estrechos de ambientes secos y de suelos derivados de rocas calcáreas, *C. scorzonerifolia* es habitante de bosques de encino y de coníferas, así como de la vegetación secundaria correspondiente en gran parte del territorio de México.

También se relaciona con *C. papilionacea,* pues al igual que ésta presenta coloración amarilla en parte de algunas estructuras, así como por su distribución en la Sierra Madre Oriental, aunque la primera se encuentra un poco más al norte. En contraparte, *C. madrigalii* difiere de ésta básicamente por el cáliz, las brácteas y la pubescencia del tallo; tiene semejanza con *C. arvensis,* ya que en ocasiones presenta una coloración amarilla en toda la planta, difiriendo sin embargo por las brácteas

Caracteres	C. madrigalii	C. scorzonerifolia	C. hidalgensis	C. papilionacea	C. arvensis
Tallo	decumbente a erecto, de 15 a 50 cm de largo, pubescencia blanca	erecto, de 15 a 80 cm de largo, pubescencia rojiza a morada	decumbente a erecto, de 2 a 15 cm de largo, pubescencia blanca	erecto, de 22 a 35 cm, pubescencia hirsuta con pelos suaves y cortos, estipitado-glandulosos	erecto, simple a ramificado, de 9 a 80 cm de alto, pubescente-viloso, hirsuto en la base
Hojas	enteras, de margen undulado a crenado, lanceoladas, superiores obovadas, de 0.7 a 4.7 cm de largo, de 0.2 a 1.0 cm de ancho	enteras, de margen undulado, lineares a lanceoladas a anchamente lanceoladas, de (3)4 a 10 cm de largo, de 0.4 a 0.8 cm de ancho	enteras a trilobadas, margen dentado, undulado o crispado, linear a linear lanceoladas, de 0.8 a 3.0 cm de largo, de 0.1 a 4.0(6.0) cm de ancho	enteras, oblanceoladas 2 a 6 cm largo, de 0.4 a 0.7 cm ancho	enteras, espatuladas, lanceoladas, oblongas, elipticas u obovadas, de 1.5 a 10 cm de largo, de 2 a 4 cm de ancho
Brácteas	verdes en la base, amarillas en el ápice, espatuladas a oblongas	rojas o moradas, lanceoladas, oblongas u ovadas	verdes, linear-lanceoladas	verdes en la base, amarillas en el ápice, anchamente oblanceoladas	verdes en la base, verde a rojo en el ápice, inferiores espatuladas y superiores obovadas
Inflorescencia	espiga de (2)5 a 16(30) cm de largo	espiga de 3 a 16 cm de largo	espiga compacta de 1.5 a 3 cm de largo	espiga poco densa de 3 a 6(15) cm	espiga densa, de 3 a 6(30) cm
Cáliz	amarillento en el ápice, de 18 a 22 mm de largo, hendidura abaxial de 5 a 6 mm de largo, la adaxial de 3 a 3.5 mm, de largo	amarillo con el ápice de color escarlata, de 20 a 32(36) mm de largo, hendidura abaxial de 11 mm de largo, la adaxial de 10 mm de largo	amarillo limón, de 15 a 23 mm de largo; hendiduras abaxial y adaxial de 5 a 8 mm de largo	amarillento, ápice amarillo-verdoso, de 17 a 24 mm de largo, , hendiduras de 9 a 10 mm redondeados	verde obscuro en el ápice, de 9 a 20 mm de largo, hendidura abaxial 4 a 7 mm, adaxial 4.5 a 5 mm.
Corola	de 20 a 26 mm de largo, labio inferior membranáceo a petaloide, 3-dentado, el diente central de 0.5 a 1.5 mm de largo, los laterales de 1 a 1.5 mm de largo	de (20)26 a 43 mm de largo, labio inferior membranáceo verde, sus dientes de 0.5 a 1.5 mm de largo	de 20 a 28 mm de largo, labio inferior 3-dentado petaloide, de 2 a 5 mm de largo	23 a 27 mm de largo, margen amarillo labio inferior 3-dentado, dientes gruesos de ca. 1 mm largo	generalmente inclusa, de 10 a 24 mm, margen dentado de 1 a 2 mm de largo con un par de callosidades en la base

Tabla 1. Características comparativas de *Castilleja madrigalii* y algunas especies relacionadas.

anchamente oblanceoladas, la pubescencia del tallo, las hendiduras más grandes del cáliz, las hojas y la densidad de flores en la inflorescencia. En la tabla 1 se enlistan algunas de las características diferenciales entre estas tres especies.

Figura 2. *Castilleja madrigalii.* Fotografía de Eleazar Carranza.

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NEW NOMENCLATURAL COMBINATIONS FOR BLUE DICKS (*DIPTEROSTEMON CAPITATUS*; ASPARAGACEAE: BRODIAEOIDEAE)

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ABSTRACT

Dichelostemma capitatum (Benth.) Alph.Wood, traditionally treated as one of five geophyte species included in *Dichelostemma* Kunth, a genus endemic to the western USA and northern Mexico, has been the subject of nearly perpetual taxonomic confusion since the early 19th century. In this paper, I review the errors that perpetuated the misapplication of names to *D. capitatum*, resurrect *Dipterostemon* Rydb. as the alternative genus for *D. capitatum*, and propose new infraspecific combinations. *Dichelostemma pulchellum* (Salisb.) A. Heller, a name persistently misapplied to *D. capitatum*, is a confused name that is synonymous with *D. congestum* (Sm.) Kunth. **Dipterostemon capitatus** (Benth.) Rydb. subsp. **pauciflorus** (Torr.) R.E. Preston, **comb. nov.**, and **D. capitatus** (Benth.) Rydb. subsp. **lacuna-vernalis** (L.W. Lenz) R.E. Preston, **comb. nov.**, are proposed.

The genus *Dichelostemma* traditionally has consisted of five geophyte species endemic to the western USA and northern Mexico (Pires 2002; Pires & Keator 2012). Phylogenetic studies place *Dichelostemma* in the Themidaceae (Fay & Chase 1996; Fay et al. 2000; Pires et al. 2001; Pires & Sytsma 2002) and more recently in the subfamily Brodiaeoideae of the Asparagaceae (Chase et al. 2009; Steele et al. 2012; Chen et al. 2013). These studies also indicate that *Dichelostemma* is not monophyletic; *Dichelostemma capitatum* (Benth.) Alph.Wood is sister to the clade that includes *Brodiaea* and the other four species of *Dichelostemma*. *Dichelostemma capitatum* has been the subject of nearly perpetual taxonomic confusion since the early 19th century, so much so that Keator (1992) dubbed it a "problematic" species. In this paper, I review the errors that perpetuated the misapplication of names to *D. capitatum*, resurrect an alternative name for *D. capitatum*, and propose new infraspecific combinations.

The source of the taxonomic confusion stems from a botanical rivalry between Richard Salisbury and James Smith that took place in the early part of the 19th Century (Britten 1886; Mabberly 1985; Preston 2013). Salisbury (1808a) described a new genus, *Hookera* Salisb., with two new species, *H. coronaria* Salisb. and *H. pulchella* Salisb., based on specimens collected in 1792 by Archibald Menzies, naturalist aboard the H.M.S. Discovery during Vancouver's explorations in the vicinity of Puget Sound and the San Juan Islands. Salisbury provided a diagnosis for *H. pulchella* but did not publish a full description until later that year (Salisbury 1808b). Shortly after Salisbury's initial publication, James Smith completed his own alternative treatment of these taxa, based on the same specimens but also on Menzies' field notes. Smith presented his description of *Brodiaea* Sm., with two species, *B. grandiflora* Sm. and *B. congesta* Sm., in a paper read before the Linnean Society on April 19, 1808, but his description of *Brodiaea* did not make it into print until two years later (Smith 1810). Despite having priority of publication, *Hookera* appears to have been suppressed in favor of *Brodiaea*, apparently for various personal and social reasons. When Kunth (1843) later proposed the segregate genus *Dichelostemma* (Greek, "bifid corona"), based on the densely clustered inflorescence and the shape of the perianth appendages, he cited *B. congesta* as the basionym, not *H. pulchella,* which he cited as a synonym.

Salisbury made several errors in his description of *Hookera pulchella*, which suggests that he rushed his species description into print in an effort to upstage Smith and to further his own botanical legacy (Preston 2013). Salisbury's initial error was to state that Menzies had collected the specimens in California, whereas Menzies (1923, p. 42) explicitly described collecting the specimens at Restoration Point, which is located on what is now Bainbridge Island in the state of Washington. Because *D. capitatum* and *D. congestum* (Sm.) Kunth both occur in California but *D. capitatum* does not occur in the Pacific Northwest, the incorrect collection locality appears to have led others to believe that Menzies had collected the two species growing together in California (Greene 1886; Hoover 1940). Although the Vancouver expedition overwintered in California, most of Menzies' collecting was done during the spring and summer in the Pacific Northwest.

Salisbury's second error was his claim that *Hookera pulchella* flowers are hexandrous. Salisbury provided a detailed description of *H. pulchella* and precisely described the three appendages that occur on the outer perianth lobes, but he interpreted them as three "emarginate" (i.e., with a bifid apex) filaments that had lost their anthers. Salisbury was adamant that the flowers were hexandrous and suggested that Menzies' field notes and Smith's description of flowers as triandrous were incorrect because the anthers of three stamens had fallen off before Menzies and Smith had noticed them. Salisbury reinforced his mistaken belief that *H. pulchella* was hexandrous when he and several others examined what he believed to be that species blooming in the garden of an acquaintance, and all had noticed that the plants possessed six anthers. The origin and identity of the garden plants Salisbury cited are unknown.

Salisbury's claim seems dubious, because the anthers of *Brodiaea* and *Dichelostemma* are basifixed and not deciduous. How could he have made this mistake? The first clue comes from the herbarium sheet at the British Museum bearing part of Menzies' type collection. One of the four specimens is not actually *D. congestum*; it was anotated "distinct and hexandrous" by Robert Brown, and later annotated to "*Triteleia howellii*" by James Dandy (botanist and Keeper of the Herbarium at the British Museum). It appears that Menzies collected two species growing together, just not *D. congestum* and *D. capitatum*.

Salisbury's illustration of a dissected flower of *Hookera pulchella* (Figures 1 and 2) shows six stamens clearly placed at two levels on the perianth tube, with the appendages opposite the outer perianth lobes. Because the stamens of *D. capitatum* are on the same level on the perianth tube, the appendages are opposite the inner perianth lobes, and the perianth lobes are longer than the tube, the illustration does not represent that species. Instead, the drawing appears to be a composite of *D. congestum* and at least one species of *Triteleia*. Some *Triteleia* species, including *Triteleia grandiflora* Lindl. var. *howellii* (S. Wats.) Hoover, have stamens that are inserted at two levels on the perianth, as in Salisbury's figure. Undoubtedly, Salisbury applied the name *H. pulchella* to the same specimens to which Smith had applied the name *B. congestum*, but Salisbury's description and illustration combined details of two different species.

Salisbury's errors might have had little impact, except for the subsequent discovery of a new species from California superficially resembling *D. congestum* but possessing six stamens. Theodor Hartweg, collecting in the vicinity of Monterey Bay in 1848, returned with specimens that were the type of the species *Brodiaea capitata* Benth. In the protologue, Bentham (1857) cited several other collections of the species from California by David Douglas, Thomas Coulter, and John Bigelow, and from Oregon by John Jeffrey. Additional collections from California were made during the Pacific Railroad surveys. Torrey (1856a, 1856b) contributed to the confusion by initially misapplying the name *Brodiaea congesta* to collections of hexandrous specimens from southern California. Subsequent generations of botanists weighed in with different opinions over the taxonomic distinction between *Brodiaea* and *Dichelostemma* and whether *pulchellum* or *capitatum* was the correct epithet for the hexandrous species, resulting in a tangle of nomenclature.

Although the debate over recognizing a broadly circumscribed *Brodiaea* vs. recognizing several smaller segregate genera continued for many years, many botanists accepted *Dichelostemma capitatum* as the hexandrous species from California, albeit under several generic names and with continued uncertainty as to the species with which to place *H. pulchella* in synonymy (Bentham 1857; Torrey 1859; Wood 1869; Baker 1871; Watson 1879; Britten 1886; Jepson 1922; Abrams 1923). A notable exception was E.L. Greene, the first California botanist to contribute to the discussion and whose views greatly added to the confusion. Greene (1886) proposed that three segregate genera, *Hookera*, *Brodiaea*, and *Triteleia* be recognized, but based on his interpretation of the rule of priority (see Article 11.3 of the International Code of Botanical Nomenclature [ICBN]; McNeill et al. 2012), he applied the genus name *Hookera* to the species currently placed in *Brodiaea* (based on *Brodiaea grandiflora*) and the genus name *Brodiaea* to the species currently placed in *Dichelostemma* (based on *Brodiaea congesta*). Greene interpreted Salisbury's statements about *H. pulchella* having six stamens at face value, i.e., that *D. pulchellum* and *D. congestum* were not the same taxon. This was based on his having observed *D. capitatum* and *D. congestum* growing sympatrically, coupled with his presumption that Menzies had collected his specimens under similar circumstances. Greene further muddied the waters when he proposed that *B. pulchella* (Salisb.) Greene and *B. capitata* were separate hexandrous species. After *Brodiaea* was proposed as a conserved name (Harms 1904) and accepted as such by the International Botanical Congress at Vienna in 1905, Heller (1906) contributed the new combination, *Dichelostemma pulchellum* (Salisb.) A. Heller.

Although Jepson (1922) and Abrams (1923) took different positions on the generic circumscription of *Brodiaea*, both rejected Greene's interpretation of *Dichelostemma pulchellum* and treated it synonymously with *D. congestum*. As these were the early major floristic works for the Pacific Coast states, the issue should have been settled. However, in his monograph of *Dichelostemma,* Hoover (1940) unfortunately resurrected Salisbury's erroneous figure of *H. pulchella* as the basis for recognizing *D. pulchellum* as the correct name for the hexandrous species, with *D. capitatum* in synonymy. Subsequently, later regional floras (Kearney & Peebles 1951; Munz 1959; Shreve & Wiggins 1964; Reveal 1977) as well as many local floras followed Hoover in misapplying the name *D. pulchellum* to the hexandrous species.

It required another monograph of *Dichelostemma* (Keator 1968, 1991) to point out Salisbury's errors and clarify that *D. capitatum* was the correct name for the hexandrous species and that *D. pulchellum* and *D. congestum* are synonymous. Because *Hookera pulchella* was published before *Brodiaea congesta*, the name *Dichelostemma pulchellum* would have priority over *Dichelostemma congestum* (Article 11.4 of the ICBN). However, because *Brodiaea pulchellum* and *Dichelostemma pulchellum* have been widely and persistently misapplied to the hexandrous species *D. capitatum*, they are to be maintained in current usage until a proposal to deal with the situation under Art. 14.1 or 56.1 has been submitted and rejected (following ICBN Article 57.1). Both *The Jepson Manual* (Keator 1993; Pires & Keator 2012) and the *Flora of North America* (Pires 2002) treatments of *Dichelostemma* have followed Keator's monograph.

Because *Dichelostemma capitatum* is the only hexandrous species in the genus, Baker (1871) proposed moving it to the hexandrous genus *Muilla*. On the same basis, Rydberg (1912) proposed placing the species in its own genus, *Dipterostemon*, into which he also placed three other taxa now treated as synonyms or subspecies of *Dichelostemma capitatum*. Rydberg's argument that the possession of six stamens was sufficiently diagnostic to warrant segregation of this new genus may seem weakly justified. However, *D. capitatum* possesses multiple other characters that further differentiate it from other *Dichelostemma* species. Hoover (1940) observed that *D. capitatum* produces cormlets at the base of the corms and at the ends of short stalks, whereas all other species of *Dichelostemma* produce cormlets only at the base of the corm. Keator (1968) noted additional differences between *D. capitatum* and the other species of *Dichelostemma* in leaf width, pubescence

of the scape, arrangement of tracheids in the stem, shape of the seed coat cells, and seed germination pattern. Keator (1991) also noted that *D. capitatum* does not hybridize with other *Dichelostemma* species, whereas the other species do hybridize with each other. In *D. capitatum*, the six stamens are united at the base of the filaments into a short staminal tube via fusion of the connective tissue, a feature not present in the other species of *Dichelostemma* (Lenz 1976). Moreover, the staminal tube possesses six lanceolate appendages that extend upward and cover the anthers and style, similar to but not homologous to the corona found in other species of *Dichelostemma*, which is an extension of the perianth (Lenz 1976).

Berg (1996) proposed resurrecting *Dipterostemon* on the basis of embryology. Although the embryology of *Brodiaea* and *Dichelostemma* is quite similar, the inner integument of the ovule of *D. capitatum* consists of two cell layers, similar to that of *Muilla* and *Triteleia* but different from the multilayered inner integument that represents a synapomorphy of *Brodiaea* and the other *Dichelostemma* species (Berg 1978, 1996, 2003).

Morphological evidence for recognizing *Dipterostemon* is fully supported by molecular data, which show that *D. capitatum* is sister to a clade composed of *Brodiaea* and the other species of *Dichelostemma* and that *Dichelostemma* is only monophyletic if *D. capitatum* is excluded (Pires et al. 2001; Pires & Sytsma 2002; Nguyen et al. 2008; Steele et al. 2012). Accordingly, a revised treatment of *Dichelostemma capitatum* is presented here that treats the species and its infraspecific taxa under the genus *Dipterostemon*.

TAXONOMIC TREATMENT

DIPTEROSTEMON Rydb., Bull. Torrey Bot. Club 12: 110. 1912. **TYPE**: *Brodiaea capitata* Benth., Pl. Hartw. 339. 1857.

DIPTEROSTEMON CAPITATUS (Benth.) Rydb., Bull. Torrey Bot. Club 12: 111. 1912. *Brodiaea capitata* Benth., Pl. Hartw. 339. 1857. *Dichelostemma capitatum* (Benth.) Alph.Wood, Proc. Acad. Nat. Sci. Philadelphia 20: 173. 1868. *Milla capitata* (Benth.) Baker, J. Linn. Soc., Bot. 11: 381. 1870. *Hookera capitata* (Benth.) Kuntze, Revis. Gen. Pl. 2: 712. 1891. **TYPE: USA. California.** "In silvis prope Monterey," *Hartweg* 2000 (holotype: K000802775[digital image!]).

   Brodiaea insularis Greene, Bull. Calif. Acad. Sci. 2: 134. 1886. *Dichelostemma insulare* (Greene) Burnham, Muhlenbergia 3: 74. 1907. *Dipterostemon insularis* (Greene) Rydb., Bull. Torrey Bot. Club 12: 110. 1912. *Brodiaea capitata* Benth. var. *insularis* (Greene) J.F. Macbr., Contr. Gray Herb. 56: 9. 1918. **TYPE.** Not located. (Note: Greene [1886] cited his earlier observation of *B. capitata* on Guadalupe Island in April, 1885, as the basis of his description, but although Greene reports having collected corms from there and growing them out at Berkeley, no record of a specimen could be found at CAS, NDG, or UC.)

   "Hookera pulchella" auct. non Salisb.: Greene, Bull. Calif. Acad. Sci. 2: 133. 1886; A.Heller, Muhlenbergia 1: 132. 1906; Rydb., Bull. Torrey Bot. Club 12: 111. 1912; Hoover, Amer. Midl. Naturalist 24: 471. 1940; C.V. Morton, Herbertia 7: 81. 1941; Reveal, Taxon 32: 294. 1983.

DIPTEROSTEMON CAPITATUS (Benth.) Rydb. subsp. **CAPITATUS**
   Dipterostemon capitatus subsp. *capitatus* (Fig. 3) is widespread throughout the California Floristic Province in California and Oregon. The populations are highly variable, and further study is needed to determine whether additional taxa can be distinguished morphologically and geographically (Preston 2014).

Dipterostemon capitatus (Benth.) Rydb. subsp. **pauciflorus** (Torr.) R.E. Preston, **comb. nov.**
Brodiaea capitata Benth. var. *pauciflora* Torr., Rep. U.S. Mex. Bound., Bot. 218. 1858. *Milla capitata* Baker var. *pauciflora* (Torr.) Baker, J. Linn. Soc., Bot. 11: 381. 1870. *Dichelostemma pauciflorum* Standl., Contr. U.S. Natl. Herb. 13: 179, 227. 1910. *Dipterostemon pauciflorus* (Torr.) Rydb., Bull. Torrey Bot. Club 12: 110. 1912. *Hookera pauciflora (*Torr.) Tidestr. Contr. U.S. Natl. Herb. 25: 123. 1925. *Dichelostemma capitatum* (Benth.) Alph. Wood subsp. *pauciflorum* (Torr.) Keator, Four Seasons 9: 30. 1992. SYNTYPES. **USA. New Mexico**. Near the copper mines, *Bigelow s.n.* (NY [digital image!]); **Arizona**. on the Gila River, *Parry s.n.* (NY [digital image!]). **Mexico. Sonora**. San Francisco Spring, *Capt. E.K. Smith s.n.* (NY [digital image!]).

Dipterostemon capitatus subsp. *pauciflorus* (Fig. 4) occurs in desert habitats of the southwestern USA and northern Mexico. Although the distinctiveness of this taxon has been questioned, both Hoover (1940) and Keator (1968, 1991, 1993) recognized it on the basis of morphological differences and its occurrence in desert habitats.

Dipterostemon capitatus (Benth.) Rydb. subsp. **lacuna-vernalis** (L.W. Lenz) R.E. Preston, **comb. nov.** *Dichelostemma lacuna-vernalis* L.W. Lenz, Aliso 8: 129. 1974. *Dichelostemma capitatum* (Benth.) Alph. Wood subsp. *lacuna-vernalis* (L.W. Lenz) D.W. Taylor, Fl. Yosemite Sierra 373. 2010. TYPE. **USA. California.** Sacramento Co.: Orangevale, 12 Apr 1967, *L.W. Lenz 24671a* (holotype: RSA 235779 [digital image!]; isotypes: RSA 235800, RSA 457167, RSA 457168, RSA 457169, RSA 457170, RSA 457171 [digital images!]).

Dipterostemon capitatus subsp*. lacuna-vernalis* (Fig. 5) is endemic to the western base of the Sierra Nevada foothills and adjacent Great Valley, ranging from Butte County south to Merced County (Preston 2014). The populations are restricted to a narrow elevation band between 30 and 270 m.

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Figure 1. *Hookera pulchellum*. Illustrated by William Hooker in the *Paradisus Londinensis*, 1808. The insets illustrate the open corolla, pistil, and a transverse section of the young fruit.

Figure 2. Enlargement of floral dissection in Figure 1.
The illustration shows six stamens, the longer stamens
opposite the inner perianth lobes and the shorter stamens
opposite the outer perianth lobes, with appendages on the
shorter stamens, and the perianth tube longer than the
tepals.

Figure 3. *Dipterostemon capitatus* subsp. *capitatus.* The inflorescences are characterized by dark bracts
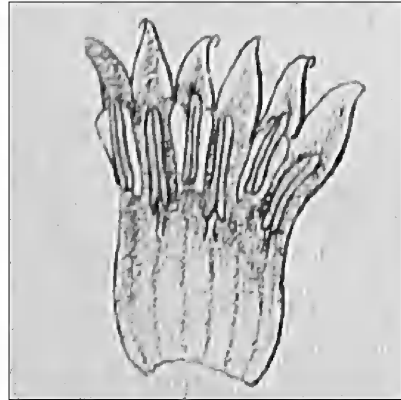and short pedicels. Photo by Steve Matson.

Figure 4. *Dipterostemon capitatus* subsp. *pauciflorus.* The inflorescences are characterized by pale bracts and long pedicels. Photo by R. Preston.

Figure 5. *Dipterostemon capitatum* subsp. *lacuna-vernalis*. The flowers are characterized by broadly ovate outer perianth lobes and very short perianth tubes (less than or equal to 4 mm). Photo by R. Preston.

MULTIVARIATE STUDIES OF *SOLIDAGO* SUBSECT. *SQUARROSAE*. I. THE *SOLIDAGO SPECIOSA* COMPLEX (ASTERACEAE: ASTEREAE)

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ABSTRACT

Solidago speciosa complex includes four taxa in *Solidago* subsect. *Squarrosae*. The complex has been treated as a single species with for varieties and as four separate species. A multivariate morphometric analyses on 265 specimens of all 14 species of subsect. *Squarrosae* and 69 specimens of the *S. speciosa* complex were carried out to assess membership in different species complexes and to assess how statistically distinct *S. jejunifolia, S. pallida, S. rigidiuscula* and *S. speciosa* were from each other. *Solidago erecta* has also been included in the complex historically. A key to the five species of the *S. speciosa* complex is presented.

Solidago subsect. *Squarrosae* A. Gray (Asteraceae: Astereae) includes 9-14 species native primarily to central and eastern Canada and the midwestern and eastern portions of the USA. Semple and Cook (2006) recognized 9 species with multiple infraspecific taxa in several species, while Semple (2016 frequently updated) recognized 14 species: *S. bicolor* L., *S. erecta* Pursh, *S. hispida* Muhl., *S. jejunifolia* Steele, *S. pallida* (Porter) Rydb., *S. porteri* Small, *S. puberula* Nutt., *S. pulverulenta* Nutt., *S. rigidiuscula* (Torr. & A. Gray) Porter, *S. roanensis* Porter, *S. sciaphila* Steele, *S. speciosa* Nutt., *S. squarrosa* Muhl., and *S. villosicarpa* LeBlond. With 14 species subsect. *Squarrosae* is the second largest subsection in the genus; *S.* subsect. *Triplinerviae* (Torr. & A. Gray) G.L. Nesom is the largest with 16 species (Semple 2016 frequently updated).

All species of subsect. *Squarrosae* include plants with erect stems arising from woody short-branched rootstocks, the basal rosette and lower stem leaves are the largest and sometimes petiolate, usually serrate, and usually oblanceolate or lanceolate. Mid and upper stem leaves are usually reduced in size upward, sessile, and serrate or entire. Inflorescence arrays vary from narrow wand-shaped forms with short branches to broader club-shaped forms with more elongated branches. In some species, the lowest branches of large inflorescences elongate forming separate wand to club shapes arrays making the array essential compound. Involucres are generally narrowly to broadly cylindrical. Phyllaries are strongly imbricate in 3-6 series and mostly lanceolate or oblong with obtuse to rounded tips that are usually appressed, except for the spreading to recurved phyllaries of *S. squarrosa*. Cypselae body indument varies from absent to sparsely to densely strigose or strigulose. All species are diploid only with the exception of *S. speciosa*, including diploids and tetraploids (Beaudry 1963; Semple et al. 1981, 1984, 1993, 2015; unpublished counts), *S. sciaphila* being tetraploid only (unpublished counts), and *S. porteri* being hexaploid only (Semple & Estes 2015). A review of chromosome counts and the cytogeography of all species of subsect. *Squarrosae* is in preparation.

The *Solidago speciosa* complex includes four taxa that were treated in a single species in Flora North America (Semple & Cook 2006) or as four separate species historically and more recently (Semple 2016 frequently updated): *S. speciosa* (Fig. 1), *S. jejunifolia* (Fig. 2), *S. pallida* (Fig. 3), and *S. rigidiuscula* (Fig. 4). *Solidago erecta* (Fig. 5) is similar to smaller plants of *S. speciosa*, in which it has been included as a variety: *Solidago speciosa* var. *erecta* (Pursh) MacMillan. *Solidago erecta* was treated as a separate species by Cronquist (1980) and Semple and Cook (2006) and is distinguished by its narrower more spiciform inflorescences and narrow mid stem leaves from the

broader showy paniculiform inflorescences and wider (>20 mm) leaves of *S. speciosa*. Thus, *S. erecta* is viewed as a peripheral member of the *S. speciosa* complex and also as part of the *S. bicolor* complex.

Figure 1. Morphology of *Solidago speciosa*: *Weatherby 7361* (NEBC) from Litchfield Co., Connecticut.

Figure 2. Morphology of *Solidago jejunifolia*: *Semple 11839* (WAT) from Cheboygan Co., Michigan.
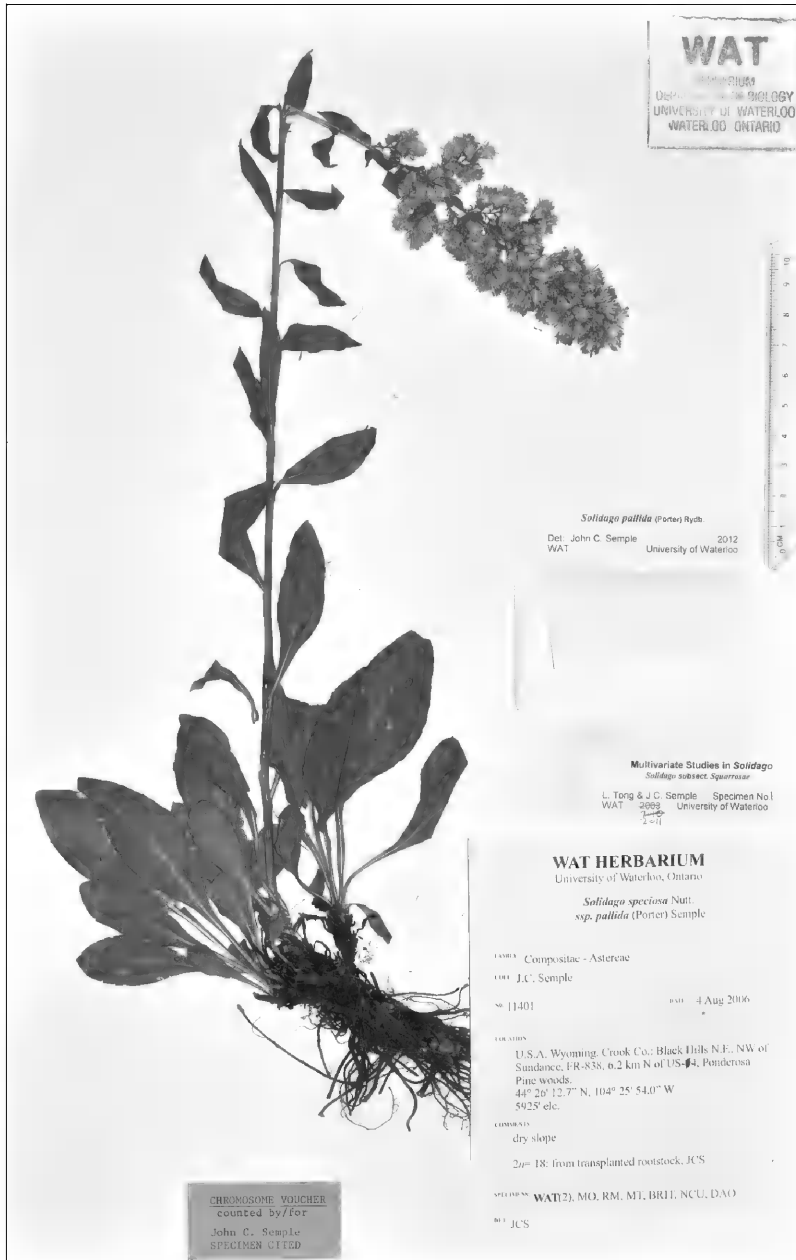
Figure 3. Morphology of *Solidago pallida*: Semple 11401 (WAT) from Crook Co., Wyoming.

Figure 4. Morphology of *Solidago rigidiuscula*: *Semple & Zhang 10602* (WAT) from Walpole Is., Ontario.

Figure 5. Morphology of *Solidago erecta*: *Semple & Suripto 9501* (WAT) from Atlantic Co., New Jersey.

There are a number of notable differences between species in the *Solidago speciosa* complex. *Solidago speciosa* produces the tallest stems (65-215 cm tall) and most robust shoots of the four species and has the largest lower stem leaves with some usually present at flowering. The inflorescence often has elongated branches and can be rather showy. The fruits are glabrous with the exception of the northeastern most population in southern Maine. Its heads vary in height, with diploids from east of the Appalachian Mts. having smaller heads than tetraploids occurring over most of the range and exclusively west of the Appalachians (Beaudry 1963; Semple et al. 1981, 1984, 1993; unpublished counts). *Solidago jejunifolia* was treated as a synonym under var. *speciosa* in Semple and Cook (2006), but field work in 2011 resulted in treating it as a separate diploid species defined by its long narrow petioles on the basal rosette and lower stem leaves which are usually present at flowering (Fig. 2). The fruits usually have some hairs on the body and generally more densely so distally. *Solidago pallida* has basal rosette and lower stem leaves like those of *S. speciosa* but usually smaller (Fig. 3) and diploid only (Semple et al. 1984; unpublished counts). Stems in general average 58 cm tall and have persistent lower stem leaves with tapering blade bases and short petioles. Upper leaves are reduced and lack serrations. Leaves are often a lighter green color than those of *S. rigidiuscula*. *Solidago rigidiuscula* includes diploids (Semple et al. 1984, 1989; unpublished counts) averaging 80 cm tall and nearly always drop the lower stem leaves by flowering (Fig. 4). Mid stem and upper leaves have few or no serrations and tend to be more congested than those of *S. jejunifolia* and *S. pallida*. Involucres of diploid *S. jejunifolia*, *S. pallida*, and *S. rigidiuscula* are smaller than those of tetraploid *S. speciosa* occurring in the ranges of the first three taxa.

The four species of the *Solidago speciosa* complex are allopatric over a significant portion of their ranges but are sympatric on the eastern prairies and in the Midwestern states. *Solidago speciosa* occurs in oak and pine woods, fields, open thickets, and along roadsides from southeastern Maine west to southeastern Minnesota and south to central Georgia, Alabama, and Mississippi in the east and northern Arkansas in the west (Fig. 6). *Solidago jejunifolia* occurs in dry sandy and gravelly soils on prairies, on sandy bluffs, and in dry open jack pine forests primarily in Minnesota, Wisconsin, and northern Michigan but extends into adjacent southeastern Manitoba (Semple et al.

Figure 6. Range of distribution of *Solidago speciosa* and locations of specimens included in the analyses.

Figure 7. Range of distribution of *Solidago jejunifolia* and locations of specimens included in the analyses.

Figure 8. Range of distribution of *Solidago pallida* and locations of specimens included in the multivariate analyses.
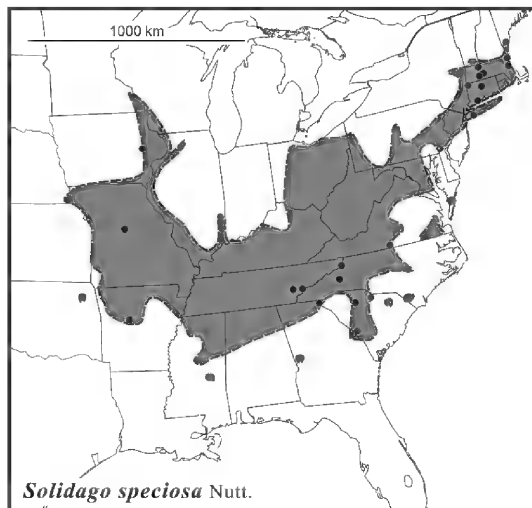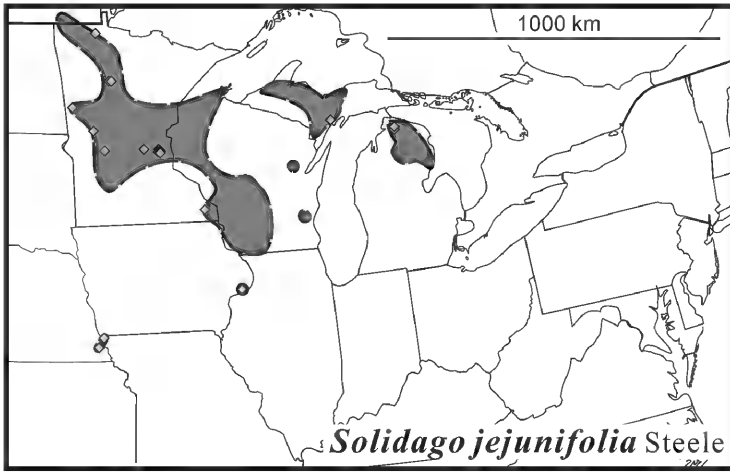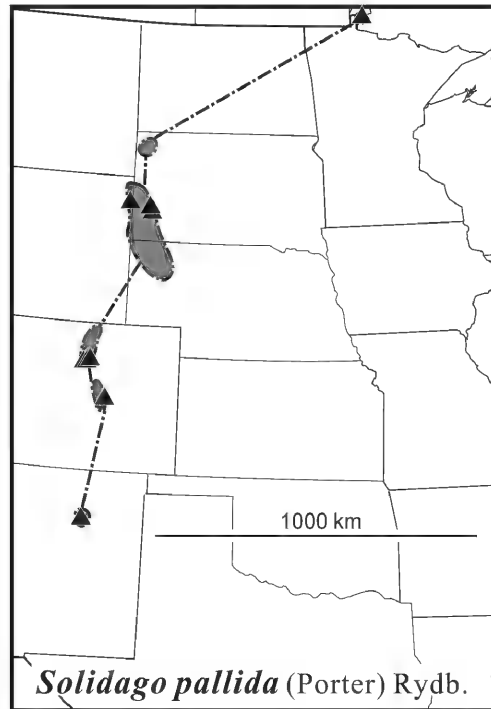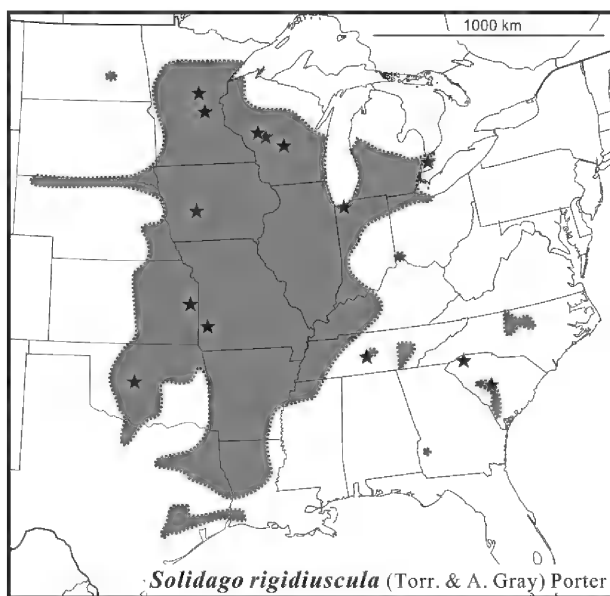
Figure 9. Range of distribution of *Solidago rigidiuscula* and locations of specimens included in the analyses.
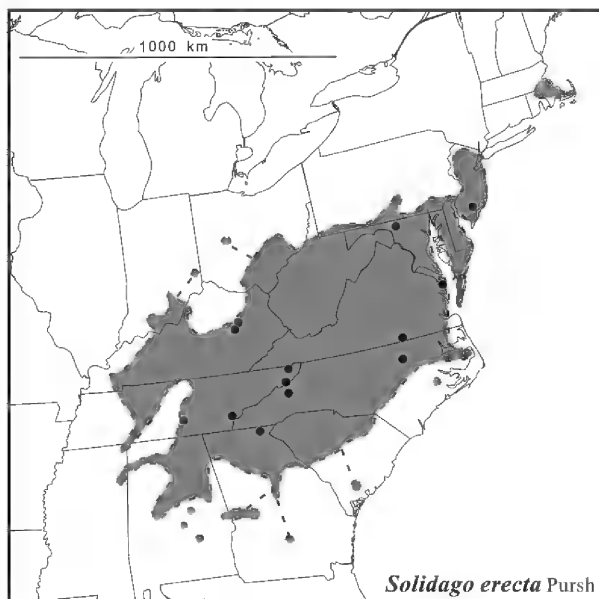

Figure 10. Range of distribution of *Solidago erecta* and locations of specimens included in the analyses.

2012) and scattered locations further to the south and west in Iowa, northwestern Missouri and adjacent Nebraska (Semple 2017; Fig. 7). *Solidago pallida* occurs in open Ponderosa pine forests in the Black Hills of eastern Wyoming and western South Dakota and along the foot hills of the Front Range of the Rocky Mountains in Wyoming, Colorado, and northern New Mexico (Fig. 8). It is also disjunct in Rainy River Dist., Ontario (Semple et al. 2012). *Solidago rigidiuscula* occurs in drier habitats in the forest prairie ecotone of the midwestern USA and scattered prairie-like habitats further east (Fig. 9). It is generally taller than *S. jejunifolia* and *S. pallida* but drops its lower stems leaves by flowering. *Solidago erecta* occurs in sandy and clay soils in open mixed oak and pine woods and along roadsides in partial to full sun. It occurs in eastern Massachusetts and adjacent Rhode Island in a disjunct area separated from the main distribution from New Jersey south to Georgia and west to southern Indiana and eastern Mississippi on in the Piedmont, central and southern Appalachians and the Cumberland and Mississippian Plateaus.

MATERIALS AND METHODS
In total, 281 specimens from A, BALT, GA, LSU, MO, the J.K. Morton personal herbarium now deposited in ROM, MT, NCU, NEBC, NY, TAWES, UNB, WAT in MT (Thiers, continuously updated) were scored and included in the analysis: *S. bicolor* (16 specimens), *S. erecta* (19 specimens), *S. hispida* (77 specimens representing 5 varieties), *S. jejunifolia* (18 specimens), *S. pallida* (12 specimens), *S. porteri* (11 specimens), *S. puberula* (16 specimens), *S. pulverulenta* (13 specimens), *S. rigidiuscula* (15 specimens), *S. roanensis* (20 specimens), *S. sciaphila* (20 specimens), *S. speciosa* (24 specimens), *S. squarrosa* (11 specimens), and *S. villosicarpa* (9 specimens). These were selected from more than 1700 specimens of *S.* subsect. *Squarrosae* examined. For each specimen, 18 vegetative and 19 floral traits were scored when possible: 1-5 replicates per character depending upon availability of material and whether or not the trait was meristic (Table 1). Basal rosette leaves were often not present. Lower stem leaves were sometimes not present. Mean values were used in the analyses, while raw values were used to generate means and ranges of variation for each trait. All traits scored are listed in Table 1.

Table 1. Traits scored for the multivariate analyses of 281 specimens of *Solidago* subsect. *Squarrosae*.

Abbreviation	Description of trait scored
STEMHT	Stem height measured from the stem base to tip (cm)
BLFLN	Basal rosette leaf length including petiole (mm)
BLFPETLN	Basal rosette leaf petiole length (not scored if winged margins broad)
BLFWD	Basal rosette leaf width measured at the widest point (mm)
BLFWTOE	Basal rosette leaf measured from the widest point to the end (mm)
BLFSER	Basal rosette leaf-number of serrations on 1 side of margin
LLFLN	Lower leaf length measured from the leaf base to tip (mm)
LLFWD	Lower leaf width measured at the widest point (mm)
LLFWTOE	Lower leaf measured from the widest point to the end (mm)
LLFSER	Lower leaf dentation-number of serrations of lower leaf
MLFLN	Mid leaf length measured from the leaf base to tip (mm)
MLFWD	Mid leaf width measured at the widest point (mm)
MLFWTOE	Mid leaf measured from the widest point to the end (mm)
MLFSER	Mid leaf dentation-number of serrations of mid leaf
ULFLN	Upper leaf length measured form the leaf base to tip (mm)
ULFWD	Upper leaf width measured at the widest point (mm)

ULFWTOE	Upper leaf measured from the widest point to the end (mm)
ULFSER	Upper leaf dentation–number of serrations of upper leaf
CAPL	Length of inflorescence (cm)
CAPW	Width of inflorescence (cm)
INVOLHT	Involucre height (mm)
OPHYLN	Outer phyllary length (mm)
OPHYLW	Outer phyllary width (mm)
IPHYLN	Inner phyllary length (mm)
IPHYLW	Inner phyllary width (mm)
RAYNUM	Number of ray florets per head
RSTRAPLN	Ray strap length top of the corolla tube to the tip of the strap (mm)
RSTRAPWD	Ray strap width measured at the widest point (mm)
RACHLN	Ray floret cypsela body length at anthesis (mm)
RPAPLN	Ray floret pappus length at anthesis (mm)
DCORLN	Disc floret corolla length from the base to tip of the corolla lobes (mm)
DLOBLN	Disc floret corolla lobe length lobe (mm)
DACHLN	Disc floret achene length at anthesis (mm)
DPAPLN	Disc floret pappus length at anthesis (mm)

All analyses were performed using SYSTAT v.10 (SPSS 2000). Details on the methodology are presented in Semple et al. (2016) and are not repeated here. Four analyses were performed. In the first analysis, all fourteen species of subsect. *Squarrosae* were included in a STEPWISE discriminant analysis. In the second analysis, eight traits with the highest F-to-remove values were used in COMPLETE discriminant analysis of all fourteen species of subsect. *Squarrosae*. In the third analysis, the four species of the *Solidago speciosa* complex were included in a STEPWISE discriminant analysis. In the fourth analysis, only specimens of *S. erecta*, *S. rigidiuscula* and *S. speciosa* were included in STEPWISE discriminant analysis. The number of specimens of each species included depended upon the traits selected.

RESULTS
The Pearson correlation matrix yielded r > |0.7| for most pairs of leaf traits reducing the number of traits to be used to either mid leaf length, mid leaf width, and mid leaf serrations. Basal rosette leaves were often absent and were not included in the discriminant analyses: basal leaf length, petiole length, and basal leaf length from widest point to tip were all highly correlated. Lower leaves were sometimes absent and lower leaf traits were excluded from discriminant analyses. Ray floret achene body length at anthesis correlated highly with disc floret achene body length and only the latter trait was included in discriminant analyses. Inflorescence length and width traits were generally used in defining a priori groups and were not included in the analyses.

Fourteen species groups analysis of subsect. *Squarrosae*
In the STEPWISE discriminant analysis of 276 specimens of fourteen species level a priori groups (*Solidago bicolor*, *S. erecta*, *S. hispida*, *S. jejunifolia*, *S. pallida*, *S. porteri*, *S. puberula*, *S. pulverulenta*, *S. rigidiuscula*, *S. roanensis*, *S. sciaphila*, *S. speciosa*, *S. squarrosa*, and *S. villosicarpa*), 13 traits selected in a STEPWISE analysis. Because there were only 9 specimens of *S. villosicarpa*, the following 8 traits were used in a COMPLETE analysis and are listed in decreasing order of F-to-remove values: ray floret lamina length (18.14), ray floret pappus length at anthesis

(16.25), number of mid stem leaf margin serrations (11.05), mid leaf length (9.70), number of ray florets (8.41), disc floret achene body length at anthesis (7.14), outer phyllary length (7.14), and (length of disc floret corolla at anthesis (5.23). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 2. F-values based on Mahalanobis distances of the between group centroids indicated the largest separations were between *S. hispida* and *S. squarrosa* (43.266), *S. rigidiuscula* and *S. squarrosa* (42.322), and *S. hispida* and *S. villosicarpa* (40.407); the smallest separations were between *S. jejunifolia* and *S. rigidiuscula* (1.795), *S. pallida* and *S. rigidiuscula* (2.552), *S. roanensis* and *S. sciaphila* (2.688), *S. puberula* and *S. pulverulenta* (3.142), *S. jejunifolia* and *S. pallida* (3.655), *S. pallida* and *S. erecta* (4.039), and *S. erecta* and *S. speciosa* (4.668). The highest average F-values were between *S. squarrosa* (33.416) and all other species and *S. villosicarpa* (27.025) and all other species.

In the Classificatory Discriminant Analysis of the fourteen putative species level a priori groups, a posteriori assignments of specimens ranged from 44-91% to their own group. The Classification matrix and Jackknife classification matrix are presented in Table 3. Only six species had percents of correct assignment in the 70-91% range: *Solidago squarrosa* with 91%, *S. pulverulenta* with 85%, *S. villosicarpa* with 78%, *S. pallida* and *S. porteri* with 73%, and *S. sciaphila* with 70%. The details are not discussed further.

Two dimensional plots of CAN1 versus CAN 3 and CAN1 versus CAN2 canonical scores for 276 specimens of all fourteen species of subsect. *Squarrosae* showed strong separate of only a few species and were not very informative due to considerable overlap in group distributions on the diagrams (Fig. 11). Eigenvalues on the first three axes were 2.913, 1.662 and 0.962. Only the symbols of *Solidago villosicarpa* and *S. squarrosa* are fairly well separated from other taxa on CAN1 versus CAN2. Symbols for the hexaploid *S. porteri* are less well separated from other species but the 95% confidence limits ellipse overlaps only slightly with the ellipse for *S. speciosa*. Symbols for *S. villosicarpa*, *S. squarrosa*, *S. porteri*, and *S. speciosa* are the only one on the right half of the CAN1 versus CAN2 diagram. Symbols for the four species of the *S. speciosa* complex (*S. jejunifolia*, *S. pallida*, *S. rigidiuscula* and *S. speciosa*) occupy the upper left quarter of the CAN1 versus CAN2 plot, but are not separated from majority of taxa on the CAN1 versus CAN3 plot. Symbols for *S. puberula* and *S. pulverulenta* and their 95% confidence ellipses overlap considerable on the CAN1 versus CAN3 plot but are mostly separated from other species in the upper left portion of the diagram. Symbols for *S. bicolor, S. erecta, S. hispida,* and *S. roanensis, S. sciaphila* are not well separated in the center left portion of the CAN1 versus CAN2 plot, but with symbols of *S. bicolor* and *S. hispida* being partially separated from the other three species in the lower left portion of the CAN1 versus CAN3 plot.

Four species groups analysis of the *S. speciosa* complex
In the STEPWISE discriminant analysis of 69 specimens of four species level a priori groups (*Solidago jejunifolia, S. pallida, S. rigidiuscula*, and *S. speciosa*), the following nine traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: number of mid leaf serrations (8.97), mid leaf width (8.93), number of disc florets (6.15), ray floret lamina length (5.95), involucre height at anthesis (5.32), inner phyllary length (4.97), mid leaf length (4.61), disc achene body length at anthesis (4.13), and disc corolla length (4.04). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The F-matrix for the discriminant analysis

Table 2. Between groups F-matrix for the fourteen a priori group analysis of *S.* subsect. *Squarrosae* (df = 8 255).

Group	bicolor	erecta	hispida	jejunifolia	pallida	porteri	puberula	pulverulenta	rigidiuscula	roanensis	sciaphila
erecta	6.749										
hispida	5.036	10.293									
jejunifolia	9.656	9.380	19.041								
pallida	4.917	4.619	8.851	3.655							
porteri	12.281	7.270	24.111	10.304	9.541						
puberula	16.180	13.451	16.886	9.592	9.884	23.937					
pulverulenta	15.306	12.744	11.737	13.272	12.243	25.699	3.142				
rigidiuscula	7.103	7.284	11.845	1.795	2.552	14.218	7.363	9.016			
roanensis	6.231	12.114	9.442	14.536	8.239	22.049	9.774	12.275	9.64		
sciaphila	8.001	7.936	8.385	14.427	6.400	21.071	6.786	8.823	9.307	2.688	
speciosa	11.356	4.668	30.770	6.533	5.559	5.060	20.713	22.080	8.151	20.890	17.836
squarrosa	31.735	24.767	43.266	38.384	30.724	17.106	36.430	32.921	42.322	38.640	32.430
villosicarpa	30.507	16.307	40.407	33.653	26.092	15.355	32.963	29.861	33.800	34.051	26.968

Group (cont.)	speciosa	squarrosa
squarrosa	32.268	
villosicarpa	20.005	11.352

Wilks' lambda = 0.0187 df = 8 13 262; Approx. F= 13.2859 df = 104 1766 prob = 0.0000

is presented in Table 4. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between *S. jejunifolia* and *S. speciosa* (18.609); the smallest separation was between *S. jejunifolia* and *S. rigidiuscula* (5.523).

In the Classificatory Discriminant Analysis of the four species level a priori groups, percents of correct a posterori assignment to the same a priori group ranged from 83-100%. The Classification matrix and Jackknife classification matrix are presented in Table 5. Results are presented in order of decreasing percents of correct placement. All 15 specimens of the *Solidago rigidiuscula* a priori group (100%) were assigned a posteriori into the *S. rigidiuscula* group; 7 specimens with 90-100% probability, 4 specimens with 80-89% probability, 2 specimens with 68% and 62% probabilities, and 2 specimen with 57% and 53% probabilities (42% and 46% probabilities to *S. jejunifolia*). Twenty-two of the 24 specimens of *S. speciosa* a priori group (92%) were assigned a posteriori to the *S. speciosa* group; 19 specimens with 91-100% probability, 1 specimen with 82% probability, 1 specimen with 73% probability, and 1 specimen with 68% probability. Two specimens of the *S. speciosa* a priori group were assigned to other species: 1 specimen to *S. pallida* with 96% probability (*Potsubay 69009,* NEBC from Holyoke, Massachusetts; 2 stem 67 cm tall, missing all but the upper most lower stem leaves); 1 specimen to *S. rigidiuscula* with 87% probability (*Eames s.n.,* NEBC from "dry field along the coast," Bridgeport, Connecticut; a small plant 67 cm tall with a small

Table 3. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of four a priori groups; a posteriori placements to groups in rows.

Group	bicolor	erecta	hispida	jejunifolia	pallida	porteri	puberula	pulverulenta	rigidiuscula	roanensis	sciaphila	speciosa	squarrosa	villosicarpa	% correct
bicolor	10	0	2	1	1	0	0	0	0	2	0	0	0	0	63
erecta	0	12	1	0	1	1	0	0	2	1	0	1	0	0	63
hispida	13	4	45	0	2	0	0	2	2	3	6	0	0	0	58
jejunifolia	0	0	0	7	0	0	0	0	6	0	0	1	0	0	50
pallida	0	1	0	1	8	0	1	0	0	0	0	0	0	0	73
porteri	0	0	0	0	1	8	1	0	0	0	0	1	0	0	73
puberula	0	0	0	0	0	0	7	7	2	0	0	0	0	0	44
pulverulenta	0	1	0	0	0	0	1	11	0	0	0	0	0	0	85
rigidiuscula	0	0	0	3	2	0	0	1	8	0	0	1	0	0	53
roanensis	2	0	2	0	0	0	1	0	0	13	2	0	0	0	65
sciaphila	0	0	0	0	1	0	0	0	1	4	14	0	0	0	70
speciosa	0	4	0	3	1	3	0	0	0	0	1	12	0	0	50
squarrosa	0	0	0	0	0	0	0	0	0	0	0	0	10	1	91
villosicarpa	0	2	0	0	0	0	0	0	0	0	0	0	0	7	78
Totals	25	24	50	15	17	12	11	21	21	23	23	16	10	8	62

Jackknifed classification matrix

Group	bicolor	erecta	hispida	jejunifolia	pallida	porteri	puberula	pulverulenta	rigidiuscula	roanensis	sciaphila	speciosa	squarrosa	villosicarpa	% correct
bicolor	8	0	3	1	2	0	0	0	0	2	0	0	0	0	50
erecta	0	10	1	0	1	1	0	0	2	1	0	3	0	0	53
hispida	13	4	45	0	2	0	0	2	2	3	6	0	0	0	58
jejunifolia	0	0	0	5	1	0	0	0	6	0	0	2	0	0	36
pallida	0	1	0	2	7	0	1	0	0	0	0	0	0	0	64
porteri	0	0	0	0	1	8	1	0	0	0	0	1	0	0	73
puberula	0	0	0	0	0	0	6	7	3	0	0	0	0	0	38
pulverulenta	0	1	0	0	0	0	1	11	0	0	0	0	0	0	85
rigidiuscula	0	0	0	3	3	0	0	0	7	0	0	1	0	0	47
roanensis	2	0	2	0	0	0	2	0	0	12	2	0	0	0	60
sciaphila	0	0	1	0	1	0	0	0	1	6	11	0	0	0	55
speciosa	0	5	0	3	1	4	0	0	0	0	1	10	0	0	42
squarrosa	0	0	0	0	0	0	0	0	0	0	0	0	10	1	91
villosicarpa	0	2	0	0	0	0	0	0	0	0	0	0	0	7	78
Totals	23	23	52	14	19	13	11	21	24	24	20	17	10	8	57
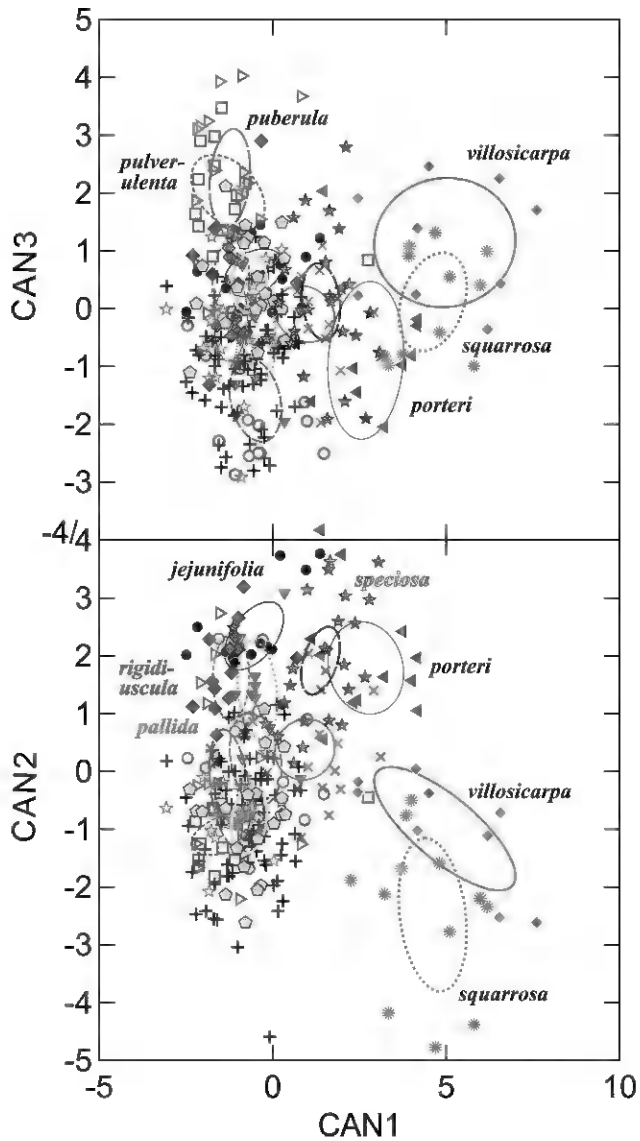
Figure 11. Plot of canonical scores (CAN1 vs CAN3 and CAN1 vs CAN2) for 276 specimens of *Solidago* subsect. *Squarrosae*: *S. bicolor* (red circles), *S. erecta* (green ×s, *S. hispida* (black +s), *S. jejunifolia* (black dots), *S. pallida* (light green triangles), *S. porteri* (red triangles), *S. puberula* (open purple triangles), *S. pulverulenta* (magenta squares), *S. rigidiuscula* (green diamonds), *S. roanensis* (open blue stars), *S. sciaphila* (pink pentagons), *S. speciosa* (yellow stars), *S. squarrosa* (red star bursts), and *S. villosicarpa* (light blue diamonds).

Table 4. Between groups F-matrix for the four a priori group analysis (df = 9   89).

Group	jejunifolia	pallida	rigidiuscula
pallida	10.099		
rigidiuscula	5.523	7.173	
speciosa	18.609	8.262	12.420

Wilks' lambda = 0.0631 df = 9 3 65; Approx. F= 9.7471 df = 27   167 prob = 0.0000

Table 5. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of four a priori groups; a posteriori placements to groups in rows.

Group	jejunifolia	pallida	rigidiuscula	speciosa	% correct
jejunifolia	15	0	3	0	83
pallida	1	10	1	0	83
rigidiuscula	0	0	15	0	100
speciosa	0	1	1	22	92
Totals	16	11	20	22	90

Jackknifed classification matrix

Group	jejunifolia	pallida	rigidiuscula	speciosa	% correct
jejunifolia	14	0	3	1	78
pallida	2	9	1	0	75
rigidiuscula	2	0	12	1	80
speciosa	0	2	1	21	88
Totals	18	11	17	23	81

inflorescence 6.2 cm tall). Fifteen of the 18 specimens of the *S. jejunifolia* a priori group (83%) were assigned a posteriori to the *S. jejunifolia* group: 11 specimens with 97-100% probability, 2 specimens with 82-83% probability, 1 specimen with 77% probability; and 1 specimen with 68% probability (15% to *S. speciosa*, and 9% each to *S. pallida* and *S. rigidiuscula*). Three specimens of the *S. jejunifolia* a priori group were assigned a posteriori to the *S. rigidiuscula* group: 2 with 83-84% (*Smith 14946* MIN from Houston Co., Minnesota, a 47 cm tall shoot with few leaves and one long petioled lower stem leaf; *Heitlinger 790* MIN from Anoka Co., Minnesota, a 55 cm tall shoot with few leaves along the entire stem and basal rosette and lower stem leaves with long petioles grading into the long tapering blade bases), and 1specimen with 58% to *S. rigidiuscula* (42% to *S. jejunifolia*; *Converse 1906* MIN from Pope Co., Minnesota; a 48 cm tall plant with basal rosette and lower stem leaves with long thin petioles typical of *S. jejunifolia*). Ten of the 12 specimens of the *S. pallida* a priori group (83%) were assigned a posteriori to the *S. pallida* group: 9 with 97-100% probability and 1 with 80% probability. Two specimens of the *S. pallida* a priori group were assigned a posteriori to other groups: 1 specimen was assigned to *S. jejunifolia* with 50% probability (38% to *S. pallida* and 9% to *S. rigidiuscula*; *Semple 11304* WAT from Pennington Co., South Dakota, a 68 cm tall shoot with large lower stem leaves and a 23 cm tall inflorescence; a smaller second shoot with much

smaller lower stem leaves from the same population and collection was assigned to *S. pallida* with 98% probability); and 1 specimen was assigned to *S. rigidiuscula* with 65% probability (18% to *S. jejunifolia* and 17% to *S. pallida*; *Semple 11304,* WAT from Pennington Co., South Dakota, a third sample from the same population and collection as above, a 43 cm tall shoot with large lower stem leaves, the lowest with a short petiole).

Two dimensional plots of CAN1 versus CAN3 and CAN1 versus CAN2 canonical scores for 69 specimens of *Solidago jejunifolia*, *S. pallida*, *S. rigidiuscula*, and *S. speciosa* are presented in Figure 12. Eigenvalues on the first three axes were 3.259, 1.099 and 0.774.
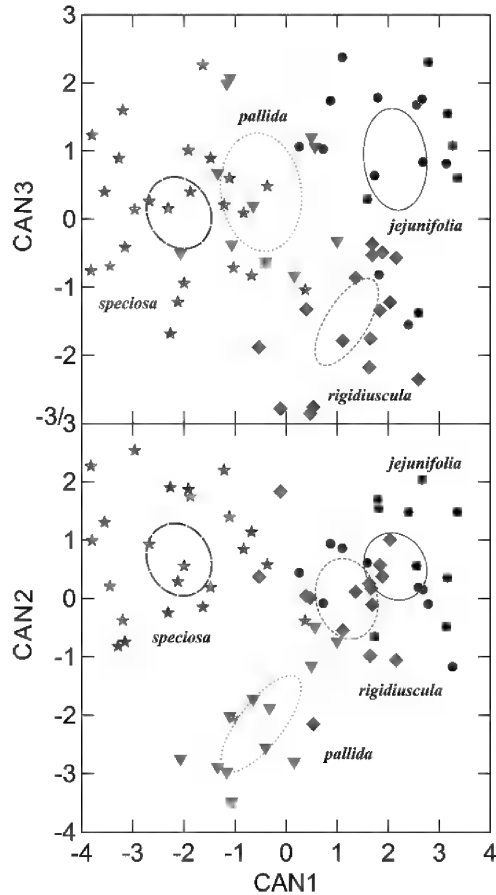

Figure 12.   Plot of canonical scores (CAN1 vs CAN3 and CAN1 vs CAN2) for 69 specimens of subsect. *Squarrosae*: *S. jejunifolia* (black dots), *S. pallida* (light green triangles), *S. rigidiuscula* (green diamonds), and *S. speciosa* (yellow stars).

Three species groups analysis of the *S. speciosa* complex
        In the STEPWISE discriminant analysis of 56 specimens of three species level a priori groups (*Solidago erecta*, *S. rigidiuscula*, and *S. speciosa*), the following eight traits selected in a STEP-WISE analysis are listed in order of decreasing F-to-remove values: disc corolla lobe length (9.72), number of disc florets (9.17), ray floret lamina length (6.09), mid leaf width (5.55), disc floret pappus length at anthesis (4.63), upper leaf width (4.30), inner phyllary length (4.01), and number of mid leaf serrations (4.00).   Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 6.   F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between *S. erecta* and *S. rigidiuscula* (15.915); the smallest separation was between *S. erecta* and *S. speciosa* (10.010).

Table 6. Between groups F-matrix for the four a priori group analysis (df = 6   46).

Group	erecta	rigidiuscula
rigidiuscula	15.915	
speciosa	10.010	14.895

Wilks' lambda = 0.0933 df = 8 2 53; Approx. F= 13.0797 df = 16 92 prob = 0.0000

        In the Classificatory Discriminant Analysis of the three species level a priori groups, percents of correct a posterori assignment to the same a priori group ranged from 78-100%. The Classification matrix and Jackknife classification matrix are presented in Table 7. Results are presented in order of decreasing percents of correct placement. All 15 specimens of the *S. rigidiuscula* a priori group (100%) were assigned a posteriori into the *S. rigidiuscula* group; 12 specimens with 100% probability, 2 specimens with 98-99% probability, and 1 specimen with 95%. Twenty of the 23 specimens of *S. speciosa* a priori group (87%) were assigned a posteriori to the *S. speciosa* group; 17 specimens with 91-100% probability, 2 specimens with 89% and 82% probabilities, and 1 specimen with 57% probability (39% to *S. erecta* and 4% to *S. rigidiuscula*). Three specimens of the *S. speciosa* a priori group were assigned to *S. erecta*: 1 specimen with 80% probability (*Semple & Chmielewski 6103,* WAT from Lancaster Co., South Carolina; 177 cm tall shoot with 39 × 8 cm inflorescence and wilted or dropped lower stem leaves; this was placed into *S. speciosa* with 98% probability in the four species analysis above); 1 specimen with 74% probability (26% to *S. speciosa*; *Semple 11675,* WAT from Union Co., South Carolina; 135 cm tall shoot with petiolate 172 × 35 mm lower stem leaves and a 49 × 5 cm inflorescence), and 1 specimen with 42% (42% to *S. speciosa* and 16% to *S. rigidiuscula*; *Eames s.n.,* NEBC from Bridgeport Connecticut; a 65 cm tall shoot with a small 6 × 2 cm inflorescence and a second upper stem with a 34 × 8 cm inflorescence and an upper stem thicker than the basal stem of the small shoot). Fourteen of the 18 specimens of the *S. erecta* a priori group (78%) were assigned a posteriori to the *S. erecta* group: 13 with 97-100% probability and 1 with 50% probability (49% to *S. rigidiuscula*). Four specimens of the *S. erecta* a priori group were assigned a posteriori to the other groups: 1 specimen was assigned to *S. rigidiuscula* with 86% probability (13% to *S. erecta* and 1% to *S. speciosa*; *Semple & Ringius 7659,* WAT from Washington Co., Maryland; a 54 cm tall shoot with small narrow upper leaves and a 15 × 2 cm inflorescence); 1

specimen was assigned to *S. rigidiuscula* with 71% probability (15% to *S. erecta* and 15% to *S. speciosa*; *Cook et al. C-589,* WAT from Monroe Co., Tennessee; a 69.5 cm tall shoot with greatly reduced upper stem leaves and 8.5 × 3 cm inflorescence); 1 specimen assigned to *S. speciosa* with 70% probability (30% to *S. erecta*; *Semple & Suripto 9688,* WAT from Mt. Mitchell, Yancy Co., North Carolina; a 53 cm tall shoot with 12 × 2 cm inflorescence); and 1 specimen assigned to *S. speciosa* with 53% probability (47% to *S. erecta*; *Semple & Chmielewski, 5984* WAT from Northumberland Co., Virginia; a 89 cm tall shoot with 28-39 mm wide lower stem leaves, greatly reduced upper stem leaves, and a 36 × 2.5 cm inflorescence).

Table 7. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of three a priori groups; a posteriori placements to groups in rows.

Group	*erecta*	*rigidiuscula*	*speciosa*	% correct
erecta	14	2	2	78
rigidiuscula	0	15	0	100
speciosa	3	0	20	87
Totals	17	17	22	88

Jackknifed classification matrix

Group	*erecta*	*rigidiuscula*	*speciosa*	% correct
erecta	13	3	2	72
rigidiuscula	0	15	0	100
speciosa	6	0	17	74
Totals	19	18	19	80

Two dimensional plots of CAN1 versus CAN2 canonical scores for 56 specimens of *Solidago erecta*, *S. rigidiuscula*, and *S. speciosa* are presented in Fig. 13. Eigenvalues on the first two axes were 2.946 and 1.717.
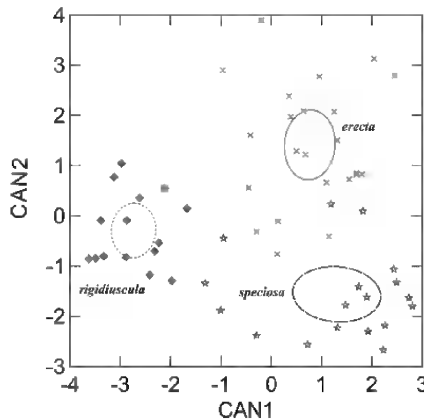

Figure 13. Plot of canonical scores (CAN1 vs CAN2) for 56 specimens of Solidago subsect. Squarrosae: *S. erecta* (green ×s), *S. rigidiuscula* (green diamonds), and *S. speciosa* (yellow stars).

DISCUSSION

The results of the first two multivariate analyses indicate that *Solidago villosicarpa*, *S. squarrosa*, and *S. porteri* are the most distinct species of the 14 species in subsect. *Squarrosae*. Ray floret lamina length had the highest F-to-remove value and ranged from a low of 1.83 (*S. bicolor*) to a high of 4.46 mm (*S. villosicarpa*): *S. squarrosa* had a mean of 3.99 mm and *S. porteri* had the next longest mean of 2.86 mm. Mean involucre height was 6.30 mm for *S. porteri*, 6.29 mm for *S. squarrosa*, and 6.13 mm for *S. villosicarpa* and ranged from 3.7-4.4 mm for all other species. However, although involucre height was selected in the STEPWISE analysis, it had a lower F-to-remove value than the eight traits that were included in the COMPLETE analysis and thus this trait was not used in generating canonical scores plotted in Fig. 11. The large involucres of the very rare *S. porteri* make it an easy species to recognize when encountered. The large involucres of *S. squarrosa* are the most distinct in subsect. *Squarrosae* due to the spreading to recurved phyllaries. The large involucres and long rays of the rare coastal southern North Carolina *S. villosicarpa* make the heads of the species the most showy in the subsection.

The results of the COMPLETE multivariate analysis indicate that other species fall into several groups. The *Solidago speciosa* complex includes *S. jejunifolia*, *S. pallida*, *S. rigidiuscula*, and *S. speciosa*, and less so *S. erecta*. The small *S. puberula* complex includes *S. puberula* and *S. pulverulenta*, which both have stems densely covered with very short hairs and are the only two species that include individuals with long narrow attenuate phyllaries. All other species are part of the *S. bicolor* complex that also includes *S. erecta*, *S. hispida*, *S. roanensis*, and *S. sciaphila*, and these species will be examined further in a manuscript on subsect. *Squarrosae* (in prep.). The *S. puberula* complex will be the subject of a third manuscript in preparation on subsect. *Squarrosae*.

The results of the second analysis strongly support the recognition of *Solidago jejunifola*, *S. pallida*, *S. rigidiuscula*, and *S. speciosa* as separate species. Each species has a range of distribution allopatric over all or part of the range. It is likely that the four species evolved as a result of vicariant biogeography events from an ancestral diploid species having moderately hairy ovaries and occurring in an interglacial period in the past that had a broad range that was reduced to four distinct refugial populations during a subsequent glacial advance in eastern North America. The locations of the refugial populations is unknown, but it seems likely that *S. pallida* evolved from the westernmost populations, while *S. speciosa* evolved from populations east of the Appalachian Mountains and *S. jejunifolia* and *S. rigidiuscula* evolved in refugial populations west of the Appalachians in the midwest or southern USA. Loss of ovary hairs occurred several times, with *S. speciosa* being the only species consistently lacking fruit hairs, except for the Maine population, which likely regained them as occurs in marginal populations. The range of *S. speciosa* west of the Appalachians is the result of the evolution of tetraploids with the ability to tolerate drier conditions of the midwestern prairies and dry open oak woods. The range of *S. rigidiuscula* from the midwest into the Carolinas likely occurred in a postglacial, drier period when prairie-adapted species expanded into the southeastern USA. Today, diploid *S. rigidiuscula* occurs in drier more prairie-like habits than *S. speciosa* in the Carolinas.

The traits of the four species of the *Solidago speciosa* complex are summarized in Table 8. Minimum, mean, and maximum values for numbers, lengths, and width of parts are included for all traits scored for the specimens included in the multivariate analyses. It is likely that individuals will be encountered with more extreme values. The raw values were used to generate the data presented. Detailed descriptions of all the four species were not included in Flora North America (Semple & Cook 2006), while the species description of *S. speciosa* included data on all four taxa treated here as separate species. Therefore the description of *S. speciosa* in Flora North America is not accurate for the species limits followed here. Basal leaf data for *S. rigidiuscula* is not included because no basal leaves were observed on herbarium sheets. Lower stem leaves of *S. rigidiuscula* were present in

limited numbers and some data is included in the table; such leaves are present on stems earlier in the season before blooming.

Table 8. Descriptive statistics on raw data on morphological traits of specimens used in the multivariate analysis *S. jejunifolia*, *S. pallida*, *S. rigidiuscula*, and *S. speciosa*: min-**mean**-max. No data for basal leaves of *S. rigidiuscula* at flowering. The lowest stem leaves are also generally absent by flowering. * traits selected in STEPDISC.

Trait	*S. jejunifolia*	*S. pallida*	*S. rigidiuscula*	*S. speciosa*
Stem height (cm)	44.5–**65.8**–82.8	32.5–**58.2**–85.8	34.3–**80.9**–120.4	65.3–**119**–215
Basal leaf length (mm)	44.5–**171**–298	55–**119.8**–240	–	65–**158**–210
Basal leaf petiole length (mm)	9–**88.7**–176	23–**45**–110	–	21–**43**–95
Basal leaf width (mm)	7–**23.5**–40	14–**22.3**–33	–	17–**37.3**–55
Basal leaf widest to tip (mm)	13–**33.5**–70	11–**31.1**–60	–	17–**36.4**–48
Basal leaf serrations (1 side)	0–**3.4**–17	0–**7.3**–20	–	7–**12.9**–27
Lower leaf length (mm)	58–**117**–205	60–**112**–215	61–**98**–153	65–**120**–181
Lower leaf petiole length (mm)	10–**47**–110	10–**23.4**–45	7–**20**–63	3–**23.8**–80
Lower leaf width (mm)	8–**18**–35	15–**27**–56	10–**18.8**–35	10–**34.4**–90
Lower leaf widest to tip (mm)	17–**30.4**–47	22–**40**–84	22–**39.0**–60	27–**52**–81
Lower leaf serrations (1 side)	0–**1.5**–7	0–**1.9**–7	0–**1.6**–9	0–**8**–21
Mid leaf length (mm)*	45–**78**–116	19–**62.5**–119	19–**62.6**–119	40–**78.8**–117
Mid leaf width (mm)*	5–**11.4**–28	3–**11.5**–19	3–**11.5**–19	5–**19.9**–38
Mid leaf widest to tip (mm)	12–**29.3**–53	10–**28.5**–40	10–**28.5**–40	17–**39.7**–67
Mid leaf serrations (1 side)*	0–**0.5**–5	0–**0.35**–5	0–**0.35**–5	0–**3.7**–13
Upper leaf length (mm)	13–**45.5**–88	14–**37.1**–57	14–**37.1**–57	17–**44.9**–79
Upper leaf width (mm)	3–**5.6**–12	2.8–**5.9**–10	2.8–**5.9**–10	2.8–**9.3**–24
Upper widest to tip (mm)	4–**19.9**–40	7–**18.6**–32	7–**18.6**–32	5–**23.8**–48
Upper serrations (1 side)	0–**0.03**–2	0	0	0–**1**–7
Inflorescence length (cm)	6.7–**18.7**–34.4	9.6–**14.8**–24.6	9.6–**14.8**–24.6	6.5–**25.3**–83
Inflorescence width (cm)	2.5–**5.4**–12.8	2.5–**4.8**–7.1	2.5–**4.8**–7.1	2–**9.9**–15
Inflor. long branch length (cm)	1.8–**4.7**–17	2–**3.9**–7	2-–**3.9**–7	1.2–**5.4**–17.5
Involucre height (mm) at anethsis*	2.5–**3.7**–4.3	3–**4.2**–5.1	3–**4.2**–5.2	3–**4.7**–7
Outer phyllary length (mm)	0.8–**1.5**–2.1	0.8–**1.35**–2.6	0.8–**1.4**–2.2	0.85–**1.5**–2.5
Inner phyllary length (mm)	2.2–**3.5**–5	2.2–**3.6**–5	2.2–**3.6**–5	1.7–**3.9**–5.7
Number of ray florets	3–0–**6.3**–12	4–**6.6**–9	4–**6.6**–9	2–**5.8**–9
Ray floret lamina length (mm)*	1.1–**2.1**–3.4	1–**2.0**–3.8	1.2–**2.0**–3.8	1.5–**2.8**–4.4
Ray floret lamina width (mm)	0.3–**0.56**–1.1	0.2–**0.62**–1.2	0.2–**0.62**–1.2	0.3–**1.0**–2.0
Ray achene body length (mm) at anthesis	0.5–**1.0**–1.4	0.6–**1.1**–1.5	0.6–**1.1**–1.5	0.6–**1.5**–2
Ray achene pappus length (mm) at anthesis	1.8–**3.1**–4	2–**2.95**–4.3	2–**2.95**–4.3	2.4–**3.6**–4
Number of disc florets*	2–**8.4**–13	4–**6.5**–9	4–**6.5**–9	5–**7.7**–15
Disc corolla length (mm)*	2.6–**3.2**–4	2.6–**3.4**–5.4	2.6–**3.4**–4.8	2.2–**4.0**–6.2
Disc corolla lobe length (mm)	0.5–**9.6**–1.6	0.5–**1.3**–2	0.5–**1.3**–2	0.75–**1.3**–2
Disc achene body length (mm) at anthesis*	0.5–**1.0**–1.3	0.6–**1.1**–1.5	0.6–**1.1**–1.5	0.6–**1.6**–2.1
Disc achene pappus length (mm) at anthesis	2.1–**4.0**–4.4	2.6–**3.4**–4.2	2.6–**3.4**–4.2	3–**1.2**–5

Number of hairs disc achene body distal half	0–**4.2**–29	0–**0.1**–3	0–**0.1**–3	0–**0.7**–41
Number of hairs disc entire achene body	0–**4.2**–29	0–**0.1**–3	0–**0.1**–3	0–**0.9**–23

Cronquist (1947) discussed *Solidago jejunifolia* under the synonym *Solidago speciosa* Nutt. var. *jejunifolia* (Steele) Cronq. (Rhodora 49: 77. 1947). As he understood the variety, it was so similar to what he treated as *Solidago speciosa* var. *pallida* Porter (Bull. Torrey Bot. Club 19: 130. 1892.) that if the ranges were not disjunct (as known at the time) that the two varieties would not be separable. He noted that Dr. L.H. Shinners had told him that var. *jejunifolia* was "more or less strong sweet-scented in the field, a condition which so far as I {Cronquist} am aware, does not obtain in the other varieties." Cronquist also noted that the inflorescence was "more open than in the other varieties, with fewer heads on longer peduncles." He suggested that var. *jejunifolia* might have been derived from var. *rigidiuscula* during postglacial xerothemic times. The results of the analyses presented here clearly show that the two species *S. jejunifolia* and *S. pallida* are statistically distinct and that their ranges likely are potentially sympatric in Minnesota or the Dakotas or were at one time.

Key to the *Solidago speciosa* complex and *S. erecta*

1. Arrays of heads either narrowly thyrsiform and often interrupted or branches well-spaced; mid cauline leaves 5–20 mm wide; Massachusetts to southern Indiana, south to Georgia and Mississippi, mostly avoiding coastal plain southward .... **Solidago erecta**
1. Arrays of head broadly thyrsiform or if narrow then congested; mid cauline leaves 3–38 mm wide; Maine to Georgia west to northwestern Ontario and adjacent Manitoba, southwest to Wyoming to New Mexico and south to Georgia in the east and eastern Texas in the west

   2. Basal rosette and lower stem leaves with narrow petioles often making up half or more of the total leaf length, present at flowering; northern Michigan to southeastern Manitoba south to eastern Iowa and northwestern Missouri and adjacent Nebraska .... **Solidago jejunifolia**
   2. Basal rosette and lower stem leaves with narrow petioles making up less than a third of the total leaf length

      3. Lowest stem leaves absent at flowering, present early to mid growing season; middle and upper stem leaves relatively numerous and overlapping .... **Solidago rigidiuscula**
      3. Lower stem leaves usually present at flowering, blades tapering to short narrow petioles

         4. Fruit body with some short hairs occurring on the upper half or over much of the fruit; Northwestern Ontario, Black Hills of South Dakota and Wyoming, stems 32–86 cm averaging 58 cm; foot hills of the Rocky Mountains in southern Wyoming to northern New Mexico .... **Solidago pallida**
         4. Fruit body hairless (except for plants from southeastern Maine); stems 65.3–215 cm averaging > 100 cm; eastern US from southeastern Maine south to Georgia west to southeastern Minnesota south to Arkansas .... **Solidago speciosa**

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VEGETATIONAL CHANGES OVER AN ELEVEN-YEAR PERIOD IN A REMNANT BLACKLAND PRAIRIE IN WALKER COUNTY, TEXAS

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ABSTRACT

Vegetational changes over an 11-year period (2005 to 2016) are recorded in a remnant blackland prairie in Walker Co., Texas using permanent vegetation monitoring plots as a basis for following future vegetation changes. This remnant prairie is privately owned and is part of working cattle and hay production ranch called Lone Oak Ranch. The remnant prairie area has been managed historically and currently to preserve and maintain this rare and globally imperiled habitat. Visually, vegetation within much of the prairie did not appear to change substantially in the 11-year period from 2005. However, along the periphery of the prairie and within the prairie itself woody encroachment has progressed substantially. Data collected in this study confirm that woody species encroachment has increased 65% from an average of 11,078 stems/ha to 18,322 stems/ha in all three plots combined. Along the periphery of the prairie, woody species increased 58% from an average of 30,501 to 48,167 stems/ha. Average absolute cover increased 79% from 177.3% to 317.7% total cover. In general, native prairie species such as little bluestem and indiangrass increased substantially while early successional native grasses such as bushy bluestem and old field three-awn decreased. Average herbaceous stem density increased 15.4% from an average of 265.3 stems/m^2 to 306.2 stems/m^2. Despite the increase in woody stems, overall, the prairie has not visually changed dramatically in the 11 years between samples.

Lone Oak Ranch includes one of the largest and most pristine (well-recovered, in part) blackland prairies known in the Pineywoods of East Texas (Keith, pers. observ.). Lone Oak Prairie is composed of approximately 120 acres of remnant and/or restored blackland prairie just west of Huntsville, Texas (Figure 1). Historical ground disturbance such as farming and intensive grazing has occurred throughout the property, but these historically disturbed areas have reverted naturally to a composition primarily of native herbaceous species typical for blackland prairies such as indiangrass (*Sorghastrum nutans*), little bluestem (*Schizachyrium scoparium*), meadow dropseed (*Sporobolus compositus*, silver bluestem (*Bothriochloa laguroides*), and Florida paspalum (*Paspalum floridanum*). Some areas have been encroached by the non-native invasive species (NNIS) King Ranch bluestem (*Bothriochloa ischaemum*); however, this species appears to be much less prominent than previously

observed and has decreased in areas where it was previously abundant. The surrounding forests are a matrix of pine-hardwood and bottomland hardwood forests with a dense shrub layer and sparse herbaceous understory.

Lone Oak Prairie is particularly susceptible to encroaching development. Interstate Hwy 45 and heavily traveled Hwy 30 to Bryan-College Station intersect less than a mile to the east of the property (Figure 1). The resulting development (including gas stations, restaurants, hotels, and a Wal-Mart) is typical of the structures found at such major intersections. A recently constructed local roadway (parallel to I-45) and the associated structures (including office buildings, retirement community, and a shopping mall) are located less than one-half mile to the east and south between I-45 and the property and are visible from the southeastern corner of the prairie. A subdivision and other residences are located less than one-half mile to the west. Some of the residences to the west are also visible from the property. To protect this rare habitat in perpetuity, the prairie, where the plots are established, was entered into a Grassland Reserve Program (GRP) conservation easement with the Natural Resources Conservation Service (NRCS) in 2007, with additional acreage being added in 2012.

The prairie habitat is defined as the Little Bluestem – Indiangrass Community Series (Texas Natural Heritage Program 1993). The plant association habitat can be more narrowly defined as the Little Bluestem – Missouri Coneflower (*Rudbeckia missouriensis*) – Narrowleaf Gumweed (*Grindelia lanceolata*) – Cusp Gayfeather (*Liatris mucronata*) Prairie or West Gulf Coastal Plain Fleming Calcareous Prairie (NatureServe 2016). This community type is ranked as a G1 community, meaning that it is considered "critically imperiled globally because of extreme rarity or because of some factor(s) making it especially vulnerable to extinction with typically 5 or fewer occurrences or very few remaining individuals (<1,000) or acres (<2,000) or linear miles (<10)" (NatureServe 2016).

In order to assess long-term vegetational changes in Lone Oak Prairie as a result of management activities and natural succession, baseline vegetation data were initially collected in three permanent Fire Monitoring Handbook (FMH) vegetation plots established in 2005 (Keith & Hyde 2006; USDI 2003) (Figures 1-4). The current study reports a 2016 re-analysis of those same plots.

MATERIALS AND METHODS

The objective of this project was to determine vegetational changes to a blackland prairie over an eleven year period (USDI 2003) by re-sampling three brush FMH vegetation monitoring plots originally established and sampled in September 2005. Data collected during this study will continue to be used to monitor long term vegetation changes in a remnant blackland prairie that occur from management activities such as prescribed burning, mowing, woody species encroachment, and climate change. Prior to initial sampling, much of the prairie was cut for hay in 2003. Subsequently, the prairie has been mowed only twice since 2005 and has not been cut for hay since 2003. Plans for controlled burns have not been implemented because of the difficulties and costs of smoke management in the surrounding development.

Plot sampling for this study was conducted on 15 and 16 September 2016. Vegetation was analyzed and quantitatively described as outlined in USDI (2003) and FEAT/Firemon Integrated (FFI) software (FFI 2009) using the following specific protocols. Data for shrub transects were collected on a 5 m wide transect. All woody species, including trees, shrubs, and woody vines, were recorded. Point-line intercepts were counted for all species, including tree species that normally exceed 2 m tall. However, woody species over 2 m in height and in the canopy above the 2 m sampling rod, but not coming into contact with the rod, were not counted. Herbaceous data were collected using a 1 m square at three locations (9 m, 19 m, and 29 m) along the 30 meter transect. Digital photographs were taken in each plot following protocols outlined in USDI (2003).

Figure 1. Fire Monitoring Handbook (FMH) vegetation monitoring plot locations on Lone Oak Ranch, part of the Grassland Reserve Program (GRP).

Plot 1 was established in a historically disturbed prairie where native herbaceous vegetation has recolonized (Figure 2). Plot 2 was established along the eastern edge of the prairie where woody species are encroaching into the grassland (Figure 3). Plot 3 was established in a near pristine portion of the prairie that is composed primarily of native herbaceous species (Figure 4). Nomenclature for species recorded in plots generally follows Diggs et al. (1999, 2006), FNA Editorial Committee (1993+), and Turner et al. (2003).

RESULTS

Table 1 shows all woody species recorded. Visually, vegetation within much of the prairie did not appear to change substantially in the 11-year period from 2005 (Figures 2 and 4). However, along the periphery of the prairie where Plot 2 is located, woody encroachment has progressed substantially (Figure 3). Data collected in this study confirm that woody species encroachment has increased 65% from an average of 11,078 stems/ha to 18,322 stems/ha in all three plots combined (Table 1). Along the periphery of the prairie in Plot 2, woody species increased from an average of 30,501 stems/ha to 48,167, an increase of 58% (Table 1). The two plots in the heart of the prairie also increased in woody stems with Plot 1 increasing 227 % from an average of 1,000 stems/ha to 3,266 stems/ha and Plot 3 woody stems increasing 104% from an average of 1,733 stems/ha to 3,533 stems/ha (Table 1). Without introduction of prescribed fires and/or mowing, this trend will most likely continue.

Table 2 shows absolute cover for all species recorded along the 30 m transects. Percentage values are absolute cover as recorded in point-line intercept transects. Absolute cover plots record all woody and herbaceous species within plots (Table 2). Average absolute cover increased 79% from 177.3% to 317.7% total cover (Table 2). These values reflect relatively dense vegetative cover with greater than one species being recorded at each 0.3 m point. An absolute cover value of 100% would indicate that an average of one species was recorded at each point. The highest cover value is recorded in Plot 1 (380%), and the lowest cover value is recorded in Plot 3 (277%) (Table 2). Average species richness (total number of species) for all plots is 34.3, increasing 23% from an average of 28 species (Table 2). In general, native prairie species such as little bluestem and indiangrass increased substantially while early successional native grasses such as bushy bluestem (*Andropogon glomeratus*) and old field three-awn (*Aristida oligantha*) decreased (Table 2). NNIS species Japanese brome increased substantially (4,150%), but King Ranch bluestem remained stable at 0.3% cover (Table 2). The large increase in cover of Japanese brome can probably be explained by above average rainfall in the spring, with 23.3 inches of precipitation occurring from February to May 2016, as compared to an average of 14.0 inches these months (NESDIS 2016). This annual species appears to fluctuate in abundance from year to year, depending on rainfall amounts (Keith, pers. observ.).

Table 3 shows herbaceous species recorded in three 1 m^2 plots. Herbaceous species recorded in plots includes all annual, biennial, and perennial species that die above ground each year and either reemerge from seed (annuals) or resprout from root bases (biennials and perennials). Herbaceous species richness and densities are often used to measure the health of ecosystems because of their susceptibility to competition from woody species encroachment in fire-suppressed habitats (Gotelli & Colwell 2001). Average herbaceous stem density recorded in plots in 2016 is 306.2 stems/m^2, increasing 15.4% from 265.3 stems/m^2 in 2005 (Table 3). The highest number of herbaceous stems was recorded in Plot 2 (321.7 stems/m^2); the lowest number of stems was recorded in Plot 3 (294.7 stems/m^2) (Table 3). Herbaceous species richness increased 5 % from an average of 33.7 species to 35.3 species (Table 3). Similarly to cover transects, Japanese brome increased 551% from 1.4 stems/m^2 to 9.3 stems/m^2. Conversely, King Ranch bluestem decreased 55% in Plot 3 (only plot it was recorded) from 4.2 stems/m^2 to 1.9 stems/m^2 (Table 3). Other notable species are highlighted in the tables (Tables 1, 2, 3).

DISCUSSION

Despite increasing woody species encroachment, the size and overall appearance of the prairie hasn't changed dramatically in the eleven years between sampling periods. Mowing of the prairie has been somewhat effective in slowing woody species encroachment; however, the overall number of woody stems has increased substantially. Continued expansion of native prairie grasses such as little bluestem and indiangrass continues but may have reduced the abundance of some forb species through interspecific competition. Both of these species greatly increased in overall cover and number of stems, while several prairie forb species have decreased. Early successional prairie species such as bushy bluestem and old field threeawn continue to decrease in abundance as the prairie continues to recover from historical ground disturbance. NNIS species are still present, but don't appear to be a threat to change the overall composition of the prairie. Japanese brome, while increasing substantially from 2005, is a small component of the overall biomass of the prairie and fluctuates greatly from year to year. Monitoring of these vegetation plots will continue to determine whether implemented management practices are effective in maintaining this imperiled habitat.

Table 1. Density (stems/ha) for all woody species recorded in plots as recorded in 30 m X 5 m plots along the 0P-30P transect. Species highlighted include those species increasing substantially highlighted in green and those decreasing highlighted in orange.

Species	Average			#1	#1	#2	#2	#3	#3
Species ↓ Year →	2005	2016	% Change	2005	2016	2005	2016	2005	2016
Berchemia scandens	689.0	977.7	41.9			2067	2933		
Celtis laevigata	89.0	177.7	99.6			267	533		
Cornus drummondii	2422.3	2133.3	-11.9			7267	6400		
Crataegus crus-gallii	244.3	311.0	27.3			733	933		
Crataegus spathulata	66.7	133.3	100.0			200	400		
Diospyros virginiana	66.7	155.7	133.5			200	467		
Forestiera ligustrina	755.7	2466.7	226.4			2267	7400		
Frangula caroliniana	177.7	100.0	-43.7			533	300		
Gleditsia triacanthos	66.7	66.7	0.0	67		133	200		
Ilex decidua	89.0	0.0	-100.0			267			
Ilex vomitoria	44.3	44.3	0.0			133	133		
Juniperus virginiana	89.0	66.7	-25.1	200		67	200		
Ligustrum sinense	44.3	89.0	100.8			133	267		
Lonicera japonica	66.7	577.7	766.5			200	1733		
Lonicera sempervirens	0.0	222.3	Inf				667		
Parthenocissus quinquefolia	0.0	22.3	Inf				67		
Pinus taeda	22.3	0.0	-100.0			67			
Prunus mexicana	22.3	22.3	0.0			67	67		
Quercus virginiana	89.0	0.0	-100.0			267			
Rubus trivialis	1399.7	3577.7	155.6	733	2933	2933	6067	533	1733
Sideroxylon lanuginosum	255.7	222.0	-13.2			300	333	467	333
Smilax bona-nox	1422.3	2533.3	78.1		133	4267	7000		467
Symphoricarpos orbiculatus	2822.0	4155.7	47.3		200	7733	11267	733	1000

Species	Average			#1	#1	#2	#2	#3	#3
Species ↓ Year →	2005	2016	% Change	2005	2016	2005	2016	2005	2016
Toxicodendron radicans	111.0	133.3	20.1			333	400		
Ulmus alata	0.0	44.3	Inf				133		
Viburnum rufidulum	0.0	22.3	Inf				67		
Vitis cinerea	22.3	44.3	98.5			67	133		
Zanthoxylum clava-herculis	0.0	22.3	Inf				67		
All species	11078.0	18322.0	65.4	1000	3266	30501	48167	1733	3533
Species Richness	9.7	10.7	10.3	3	3	23	25	3	4

Table 2. Percent absolute cover of all recorded species along a 30 m transect in all plots sampled. Cover measurements were recorded every 0.3 m along the 30 m transect. Substrate includes leaf litter, duff, rocks, and bare soil. Species highlighted include those species increasing substantially highlighted in green and those decreasing highlighted in orange.

Absolute Cover (%)	Average			#1	#1	#2	#2	#3	#3
Species ↓ Year →	2005	2016	% Change	2005	2016	2005	2016	2005	2016
Agalinis heterophylla	0.3	1.0	200.0				2.0	1.0	1.0
Ambrosia psilostachya	2.0	0.7	-66.7	3.0	2.0	3.0			
Ambrosia trifida	0.7	0.0	-100.0			2.0			
Amphiachyris dranunculoides	1.3	1.7	25.0	1.0	4.0	2.0	1.0	1.0	
Andropogon glomeratus	6.3	0.3	-94.7	5.0		7.0	1.0	7.0	
Aristida longespica	1.3	2.3	75.0	1.0	4.0	2.0	3.0	1.0	
Aristida oligantha	10.7	4.3	-59.4	23.0	11.0	9.0			2.0
Berchemia scandens	0.0	0.3	Inf				1.0		
Bothriochloa ischaemum	0.3	0.3	0.0					1.0	1.0
Bothriochloa laguroides	13.7	14.7	7.3	13.0	6.0	12.0	27.0	16.0	11.0
Brickellia eupatorioides	0.0	1.0	Inf		3.0				
Bromus japonicus	0.7	28.3	4150.0		36.0	2.0	16.0		33.0
Carex cherokeensis	5.3	16.3	206.3	9.0	25.0	2.0	23.0	5.0	1.0
Carex microdonta	2.0	17.7	783.3	3.0	44.0	2.0	8.0	1.0	1.0
Centaurea americana	0.0	1.7	Inf		3.0		2.0		
Chaerophyllum tainturieri	0.0	0.3	Inf		1.0				
Cornus drummondii	0.3	0.0	-100.0				1.0		
Croton monanthogynus	1.0	8.3	733.3	1.0	20.0	2.0	5.0		
Cuscuta indecora	2.3	0.3	-85.7			5.0	1.0	2.0	
Dalea compacta	0.0	0.3	Inf						1.0
Dalea multiflora	1.0	0.3	-66.7	1.0	1.0	2.0			
Desmanthus illinoensis	1.0	1.0	0.0		1.0	3.0			2.0

Absolute Cover (%)	Average			#1	#1	#2	#2	#3	#3
Species ↓ Year →	2005	2016	% Change	2005	2016	2005	2016	2005	2016
Dichanthelium oligosanthes spp. scribnerianum	5.3	6.0	12.5	7.0	8.0	8.0	6.0	1.0	4.0
Digitaria cognata	0.0	0.7	Inf				1.0		1.0
Echinacea sanguinea	0.0	0.3	Inf						1.0
Eragrostis hirsuta	0.0	2.0	Inf		1.0				5.0
Eragrostis intermedia	3.7	1.0	-72.7	5.0		6.0	3.0		
Euphorbia bicolor	6.0	16.0	166.7	11.0	28.0	7.0	12.0		8.0
Eustoma grandiflorum	0.0	0.3	Inf		1.0				
Fimbristylis puberla	0.0	0.7	Inf				2.0		
Galactia volubilis	0.0	0.3	Inf				1.0		
Gleditsia triacanthos	0.0	0.7	Inf				2.0		
Grindelia lanceolata	4.7	6.3	35.7	10.0	19.0	2.0		2.0	
Hedyotis nigricans	1.0	3.0	200.0		6.0	1.0	2.0	2.0	1.0
Heliotropium tenellum	0.0	1.0	Inf		3.0				
Indigofera miniata	0.3	0.0	-100.0			1.0			
Iva annua	13.3	5.3	-60.0	18.0	7.0	8.0	8.0	14.0	1.0
Liatris mucronata	0.3	0.0	-100.0					1.0	
Monarda citriodora	0.0	2.0	Inf		2.0		2.0		2.0
Muhlenbergia capillaris	0.3	0.0	-100.0			1.0			
Neptunia lutea	0.3	0.0	-100.0	1.0					
Oenothera speciosa	0.7	0.0	-100.0	1.0		1.0			
Oxalis dillenii	0.3	0.3	0.0	1.0			1.0		
Panicum capillare	0.0	3.7	Inf		11.0				
Paspalum dilatatum	0.0	2.0	Inf				4.0		2.0
Paspalum floridanum	3.7	7.0	90.9		2.0	9.0	15.0	2.0	4.0
Paspalum pubiflorum	0.0	1.0	Inf		3.0				
Paspalum setaceum	0.3	0.0	-100.0	1.0					
Phalaris caroliniana	0.0	0.7	Inf		1.0				1.0
Plantago virginica	0.0	0.3	Inf		1.0				
Rubus trivialis	2.3	7.3	214.3			7.0	15.0		7.0
Rudbeckia missouriensis	9.0	6.0	-33.3	8.0	11.0	10.0	6.0	9.0	1.0
Salvia lyrata	0.3	0.3	0.0				1.0	1.0	
Schizachyrium scoparium	28.7	68.7	139.5	5.0	36.0	30.0	79.0	51.0	91.0
Setaria parviflora	6.0	7.0	16.7	3.0	3.0	9.0	4.0	6.0	14.0
Smilax bona-nox	0.0	1.7	Inf				5.0		
Solidago altissima	2.3	2.0	-14.3	2.0	3.0	1.0		4.0	3.0
Sorghastrum nutans	9.0	27.7	207.4	6.0	29.0	2.0	12.0	19.0	42.0
Sporobolus compositus	23.0	19.7	-14.5	27.0	19.0	18.0	11.0	24.0	29.0

Absolute Cover (%)	Average			#1	#1	#2	#2	#3	#3
Species ↓ Year →	2005	2016	% Change	2005	2016	2005	2016	2005	2016
Strophostyles leiosperma	0.0	1.7	Inf				5.0		
Symphyotrichum ericoides	3.0	8.7	188.9	5.0	18.0		2.0	4.0	6.0
Symphyotrichum praealtum	0.0	2.3	Inf		6.0		1.0		
Symphoricarpos orbiculatus	2.3	2.3	0.0				7.0	6.0	1.0
Verbena halei	0.3	0.0	-100.0	1.0					
Verbena xutha	0.3	0.3	0.0	1.0	1.0				
Total	**177.3**	**317.7**	**79.1**	**173.0**	**380.0**	**184.0**	**296.0**	**175.0**	**277.0**
Species Richness	**28.0**	**34.3**	**22.6**	**28**	**37**	**33**	**37**	**23**	**29**
Substrate	**2.0**	**0.0**	**-100.0**	**4.0**	**0.0**	**1.0**	**0.0**	**1.0**	**0.0**

Table 3. Density (stems/m^2) for all herbaceous species in plots sampled as recorded in three 1 m^2 plots along the 0P-30P transect. Species highlighted include those species increasing substantially highlighted in green and those decreasing highlighted in orange.

Stems/m^2	Average			#1	#2	#2	#2	#3	#3
Species ↓ Year →	2005	2016	% Change	2005	2016	2005	2016	2005	2016
Acalypha gracilens	0.0	0.2	Inf				0.7		
Agalinis heterophylla	0.0	0.3	Inf				1.0		
Ambrosia psilostachya	2.8	0.9	-68.2	1.7	2.7	4.0		2.7	
Amphiachyris dranunculoides	1.0	1.2	22.3		2.7	2.3	1.0	0.7	
Andropogon glomeratus	5.9	0.0	-100.0	5.3		8.3		4.0	
Aristida longespica	1.8	3.9	120.2			5.3	11.7		
Aristida oligantha	52.0	8.9	-82.9	119.3	17.3	28.3		8.3	9.3
Asclepias linearis	0.0	0.1	Inf				0.3		
Asclepias viridis	0.1	0.0	-100.0	0.3					
Bothriochloa ischaemum	4.2	1.9	-55.4					12.7	5.7
Bothriochloa laguroides	4.1	9.3	127.6	1.0	5.3	4.3	16.0	7.0	6.7
Brickellia eupatorioides	1.6	0.2	-85.7	4.0	0.7	0.7			
Bromus japonicus	1.4	9.3	551.2		3.7	4.3	7.0		17.3
Carex cherokeensis	4.5	25.8	477.1	3.0	10.3	0.7	33.3	9.7	33.7
Carex microdonta	2.1	30.8	1365.7	1.0	60.7	2.6	7.7	2.7	24.0
Centaurea americana	0.0	0.9	Inf		2.0		0.7		
Chaerophyllum tainturieri	0.0	0.9	Inf		1.7		1.0		
Chamaesyce nutans	1.1	0.1	-90.0				3.3		0.3
Coreopsis tinctoria	0.3	0.0	-100.0					1.0	
Croton monanthogynus	1.1	5.0	345.1	1.7	6.3	1.7	7.7		1.0
Cuscuta indecora	5.3	0.0	-100.0				1.3	14.7	
Dalea compacta	0.3	0.2	-33.0			0.7	0.7	0.3	

Stems/m^2	Average			#1	#2	#2	#2	#3	#3
Species ↓ Year →	2005	2016	% Change	2005	2016	2005	2016	2005	2016
Dalea multiflora	3.9	2.0	-48.7	8.0	6.0	3.7			
Desmanthus illinoensis	0.3	1.4	347.4		0.7	0.7	2.7	0.3	1.0
Dichanthelium oligosanthes subsp. scribnerianum	5.3	5.6	4.1	7.7	5.3	7.0	7.3	1.3	4.0
Dichondra caroliniana	0.1	0.7	506.1			0.3	1.0		1.0
Digitaria cognata	0.0	0.8	Inf						2.3
Echinacea sanguinea	0.2	0.8	247.8			0.7	2.3		
Elymus virginicus	0.0	0.4	Inf				1.3		
Eragrostis intermedia	12.0	17.0	41.7		10.0	36.0	41.0		
Euphorbia bicolor	2.6	2.9	13.0	4.0	3.7	2.0	4.0	1.7	1.0
Eustoma grandiflorum	0.0	0.4	Inf		1.3				
Gaura brachycarpa	0.9	0.0	-100.0	2.7					
Grindelia lanceolata	1.9	1.0	-47.4	4.0	3.0	0.7		1.0	
Hedyotis nigricans	3.6	3.4	-3.2	8.3	7.3	1.7	2.0	0.7	1.0
Heliotropium tenellum	0.9	2.2	150.4	2.3	6.3			0.3	0.3
Indigofera miniata	0.3	0.1	-67.0			1.0	0.3		
Iva annua	22.8	3.8	-83.4	27.7	5.7	15.3	4.3	25.3	1.3
Liatris mucronata	0.3	0.0	-100.0					1.0	
Monarda citriodora	0.0	2.7	Inf		3.7		2.7		1.7
Neptunia lutea	1.1	0.0	-100.0	0.7		2.7			
Oenothera speciosa	1.6	4.0	155.3		4.0	4.0	5.7	0.7	2.3
Oxalis dillenii	0.7	2.8	310.3	1.3	2.3	0.7	4.3		1.7
Panicum capillare	0.0	2.3	Inf		7.0				
Paspalum dilatatum	0.3	1.7	400.0			1.0			5.0
Paspalum floridanum	3.7	2.6	-30.3			11.0	7.7		
Paspalum setaceum	1.9	0.0	-100.0			5.7			
Phalaris caroliniana	0.0	1.4	Inf		1.3		0.7		2.3
Plantago virginica	0.0	4.1	Inf		11.7				0.7
Polygonum aviculare	0.0	0.1	Inf						0.3
Polytaenia texana	0.1	0.0	-100.0			0.3			
Rudbeckia missouriensis	7.0	4.0	-42.7	4.3	8.3	5.3	1.0	11.3	2.7
Salvia azurea	0.6	0.0	-100.0			1.7			
Salvia lyrata	0.4	1.1	151.1	0.3		0.7	2.7	0.3	0.7
Schizachyrium scoparium	29.3	76.1	159.5	7.3	50.0	21.7	83.3	59.0	95.0
Setaria parviflora	6.8	4.8	-29.4	6.3		11.7	11.7	2.3	2.7
Silphium asteriscus	0.0	0.1	Inf				0.3		
Solidago altissima	3.9	2.7	-31.7	0.7	1.3	5.7	3.3	5.3	3.3
Sorghastrum nutans	8.7	8.3	-3.9	1.3	5.3	5.7	5.3	19.0	14.3

| Stems/m^2 | Average | | | #1 | #2 | #2 | #2 | #3 | #3 |
Species ↓ Year →	2005	2016	% Change	2005	2016	2005	2016	2005	2016
Sporobolus compositus	41.0	34.2	-16.5	36.3	26.7	47.0	32.7	39.6	43.3
Stylosanthes leiosperma	0.6	0.7	17.6			1.7	2.0		
Symphyotrichum ericoides	5.8	6.1	6.0	5.3	6.7	0.7	4.3	11.3	7.3
Symphyotrichum praealtum	1.8	3.7	106.4	2.3	10.0			3.0	1.0
Symphyotrichum subulatum	0.1	0.0	-100.0	0.3					
Verbena halei	5.3	0.1	-97.9	16.0	0.3				
Warnockia scutellarioides	0.0	0.1	Inf						0.3
All stems	265.3	306.2	15.4	284.5	302.3	264.1	321.7	247.2	294.7
Species Richness	33.7	35.3	5.0	30	37	42	36	29	33

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Figure 2. Plot 1: 15 September 2005 and 16 September 2016. The conspicuous, white-bracted species is *Euphorbia bicolor*.

Figure 3. Plot 2: 15 September 2005 and 15 September 2016.   Notice woody encroachment to left of view increasing from 2005 to 2016.

Figure 4. Plot 3: 30 September 2005 and 16 September 2016. Prairie grasses visually more prominent in 2016.

DESCURAINIA BROWNIAE (CRUCIFERAE), A NEW SPECIES FROM BRIAN HEAD PEAK, IRON COUNTY, UTAH

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ABSTRACT

Descurainia browniae R.P. McNeill, a new species described from Brian Head Peak, Iron County, Utah. It is most similar to *D. incana* (Bernh. ex. Fisch. & C.A. Mey.) Dorn, *D. torulosa* Rollins, and *D. kenheilii* Al-Shehbaz but can be distinguished from these species based on fruit and flower morphology and geography. Due to the known patterns and processes of island biogeography, it is likely a neoendemic to Brian Head Peak, Utah.

Descurainia Webb & Berthelot, although not one of the larger North American genera in Cruciferae/Brassicaceae, is still complex due to extensive interspecific hybridization and ruderal habit (Detling 1939; Goodson 2007; Goodson & Al-Shehbaz 2010). On 1 July 2014, I found two individuals of an unfamiliar member of the Cruciferae on a volcanic substrate on Brian Head Peak in southern Utah. I attempted to identify the taxon with the available floras, including the Flora of North America, the Intermountain Flora, and A Utah Flora (Cronquist et al. 1994; Goodson & Al-Shehbaz 2010; Welsh et al 1993). I identified it as the genus *Descurainia*, but species level identification was not satisfactory. I contacted Dr. Ihsan Al-Shehbaz at the Missouri Botanical Garden and he stated that it was possibly an undescribed taxon. I returned to the site on 2 August 2014 and made a more thorough survey of the peak. I found 46 plants and made a collection of three mature specimens. On 6 September 2014, I returned for a third visit, which resulted in finding a total of 42 plants. I collected a further seven individuals at that time. On 12 September 2015, I returned and collected a further 10 plants. None of the plants from 2014 appeared to be in existence in 2015, indicating an annual life cycle.

DESCURAINIA BROWNIAE R.P. McNeill, **sp. nov.** **TYPE**: **Utah**. Iron Co.: Brian Head Peak, Dixie National Forest, ca. 100 m S of the parking area at the end of FR 047/Brian Head Peak Rd, on S ridge below peak, on outcrop of the distinct reddish scoria band below rock band that forms the peak, rock heavily covered with yellow and orange lichens, growing in the cracks where mineral soil has accumulated, extensive signs of rodent activity (poop), 37.67965, -112.83089, main slope: 65%, (rocky outcrop where soil collects: 100%), W aspect on a south ridge, 3391 m, 12 Sept 2015, *Rick McNeill s.n.* (holotype: UTC). Figures 1–4.

Descurainia browniae superficially is most similar to *D. incana* (Bernh. ex. Fisch. & C.A. Mey.) Dorn, *D. torulosa* Rollins and *D. kenheilii* Al-Shehbaz. It can easily be differentiated from these species based on flower/fruit morphology, and disjunct geographic range.

Descurainia browniae has glabrous fruits, median filaments 0.56–0.87 mm long and is an annual, while *D. torulosa* has pubescent fruits, median filaments 1.6–2 mm long and is perennial. *Descurainia browniae* is found in southwestern Utah while *D. torulosa* is endemic to Wyoming.

Descurainia incana has 14–22 ovules per fruit, median filaments 1.4–2 mm long, distal leaf segments that are acute, and is biennial; *D. browniae* has 1–11 ovules per fruit, median filaments 0.56–0.87 mm long, distal leaf segments that are obtuse or rotund, and is an annual.

Descurainia kenheilii looks most similar to smaller specimen of *D. browniae*. Both are small *Descurainia* that occur in high elevation habitats, but these two species can easily be separated based on numerous characteristics. *Descurainia kenheilii* has fruits 1–1.3 mm wide, is not canescent, has styles 0.1–0.2 mm long, has a prominent vein on the septum of the fruit, is a perennial and only occurs in southwestern Colorado; *D. browniae* has fruit 0.53–1.00(–1.06) mm wide, is canescent, styles 0.24–0.40 mm long, no vein on the septum, is an annual and has only been found in southwestern Utah. The known range of *Descurainia browniae* is approximately 480 km from the range of *D. kenheilii* and 560 km from the range of *D. torulosa*.

Herbs, annual, eglandular, canescent, with dendritic trichomes. **Stems** 2.0–11.5 cm tall, erect, single from base, simple or multiple branched above, highly branched individuals are apparently a response to herbivory. **Leaves** basal and cauline, pinnate, obovate to ovate; basal petioles 3.5–19.3 mm long, cauline petioles 0.4–9.2 mm, blade 1.2–18.7 x 0.4–13.5 mm, lateral segments 1–4 pairs, obtuse to rounded, occasionally mucronulate, distal segments obtuse to rounded, rarely acute on smaller segments, entire; reduced upwards. **Racemes** not elongated in fruit, 11.0–81.9 mm; **fruiting pedicels** appressed may become erect or ascending at maturity, 1.07–4.46 mm, slender, straight to curved. **Flowers: sepals** obovate, ascending; at anthesis, adaxially yellow; abaxially green, dendritic trichomes 0.42–1.16 x 0.42–0.66 mm; **petals** yellow, clawed, obovate, 0.50–0.99 (1.14) x 0.30–0.67 mm; median filaments 0.56–0.87 mm long; anthers rotund, 0.18–0.32 mm long. **Fruit** linear, appressed to ascending, glabrous, 1.40–9.99 x 0.53–1.00(–1.06) mm wide, straight to slightly curved, terete; valves glabrous, torulose, with a distinct mid-vein; septum without a prominent mid-vein; style nearly obsolete 0.24–0.40 mm long; ovules and seeds 1–11 per fruit. **Seeds** reddish brown, uniseriate, asymmetrically oval or ovate, 0.90–1.34 x 0.42–0.62 mm.

Descurainia browniae flowers and fruits June-September and will fruit while only 21 mm tall. Associated species at the type locality are *Erigeron compositus* var. *glabratus*, *Poa glauca* subsp. *rupicola*, *Potentilla pensylvanica* var. *pensylvanica*, and *Ribes velutinum* var. *velutinum*. The new species is named in honor of Dr. Sara H. Brown ecologist, educator, and friend. High resolution images of the new species are available at McNeill (2017).

Descurainia browniae occurs on Brian Head Peak in southwestern Utah (Fig. 1). It is found at approximately 3391 meters elevation, 36 meters below the top of the peak in the alpine zone. It occurs on the Isom formation (26-27 mya), which is a densely welded, trachydacitic, ash-flow tuff that has been exposed by weathering of the overlaying Leach Canyon formation (23.8 mya), a poorly welded, rhyolite tuff that forms the top of Brian Head Peak (Rowey et al. 2013). At present the plants are known to occur in a single location on the west side of the south ridge. The area where this population is found is a high use location for small mammals. The site has a large amount of mammal scat and many individuals show signs of herbivory. The plants apparently respond to herbivory by transferring apical dominance and producing multiple stems. In the absence of herbivory plants appear to be single-stemmed. *Descurainia browniae* grows in microsites where mineral soil and mammal scat has accumulated in rock cracks and on flat spots on the rocky outcrop. The site is largely inaccessible except to climbing or flying animals.

Descurainia browniae is likely a neoendemic to Brian Head Peak. The small size and short growing season of *D. browniae* suggest both an annual life cycle and self-fertilizing reproduction (Snell & Aarssen 2005), but the plants also appear to reproduce continually throughout the growing season, as old fruit and new flower buds were present on the same small plants and seedlings were present when plants had mature fruit in early fall.

High elevation peaks in the desert form what are essentially island biogeographical patterns for those species restricted to the alpine environments. These patterns can easily result in the reproductive isolation of a population (Billings 1974; Kruckeburg 2002; Warshall 1995), and exert

strong selection pressures, especially for selfing (Billings 1974; Snell & Aarssen 2005). These pressures can produce marked changes, especially on short-lived, annual species that may produce multiple generations in one season and thereby accumulate changes very rapidly. When these processes of island biogeography occur in conjunction with the selection pressures of the alpine environment, endemic species, while not common, are not unexpected (Schoville et al. 2011).

Figure 1. Location of *Descurainia browniae* in Iron Co., Utah.

Figure 2. Mature plant of *Descurainia browniae* next to a automobile key. This plant has new flowers and buds lower on the stem and older septae of fruits on the upper stem.
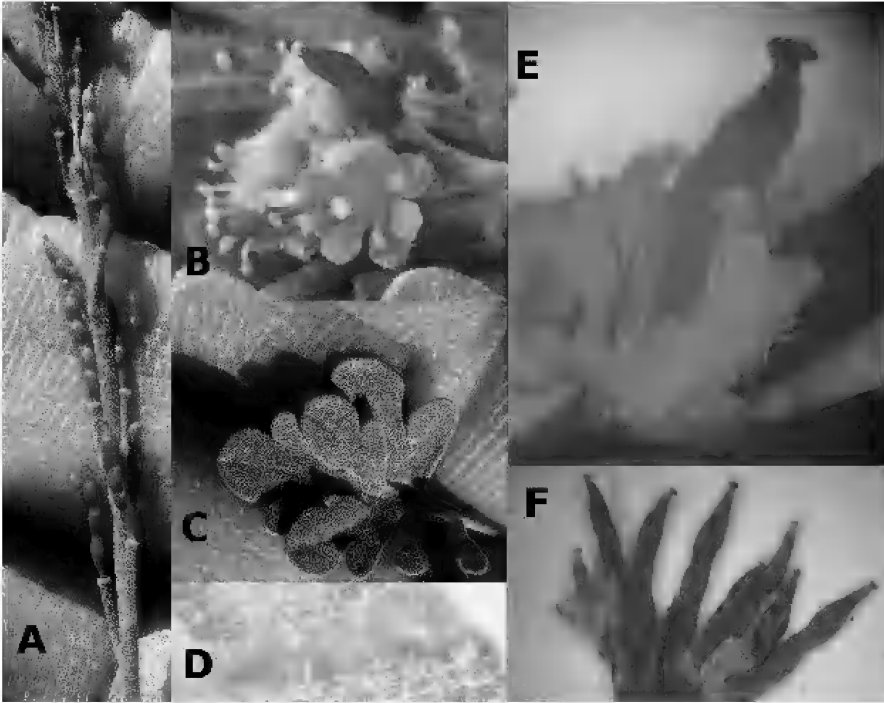
Figure 3. *Descurainia browniae*. (A) stem and fruits, (B) flowers and immature fruits, (C) canescent leaf, (D) trichomes, (E) flower and immature fruit, and (F) immature fruits

Key to selected species in *Descurainia* (mature fruit required)

1. Fruit pubescent, Wyoming endemic .... **Descurainia torulosa**
1. Fruit glabrous, not restricted to Wyoming.

  2. Fruit fusiform, not torulose .... **Descurainia californica**
  2. Fruit linear and torulose, at least slightly.

    3. Ovules ≥ 14 per fruit, ±slightly torulose, median filaments ≥ 1.4 mm long.

      4. Fruit width 0.3–0.6 mm, biennial, septum often veined .... **Descurainia incana**
      4. Fruit width 0.9–1.3 mm, annual, septum not veined .... **Descurainia incisa**

    3. Ovules ≤ 11 per fruit, torulose, median filaments ≤ 1 mm long.

      5. Torulose indentations < ¼ width of fruit when mature, fruit 1–1.3 mm wide, perennial, septum veined, plant not canescent, style 0.1–0.2 mm long, Colorado endemic
……............ .... **Descurainia kenheilii**
      5. Torulose indentations > ¼ width of fruit when mature, fruit 0.53–1.00(–1.06) mm wide, annual, septum not veined, plant canescent, style 0.24–0.40 mm long, Utah endemic
.... **Descurainia browniae**
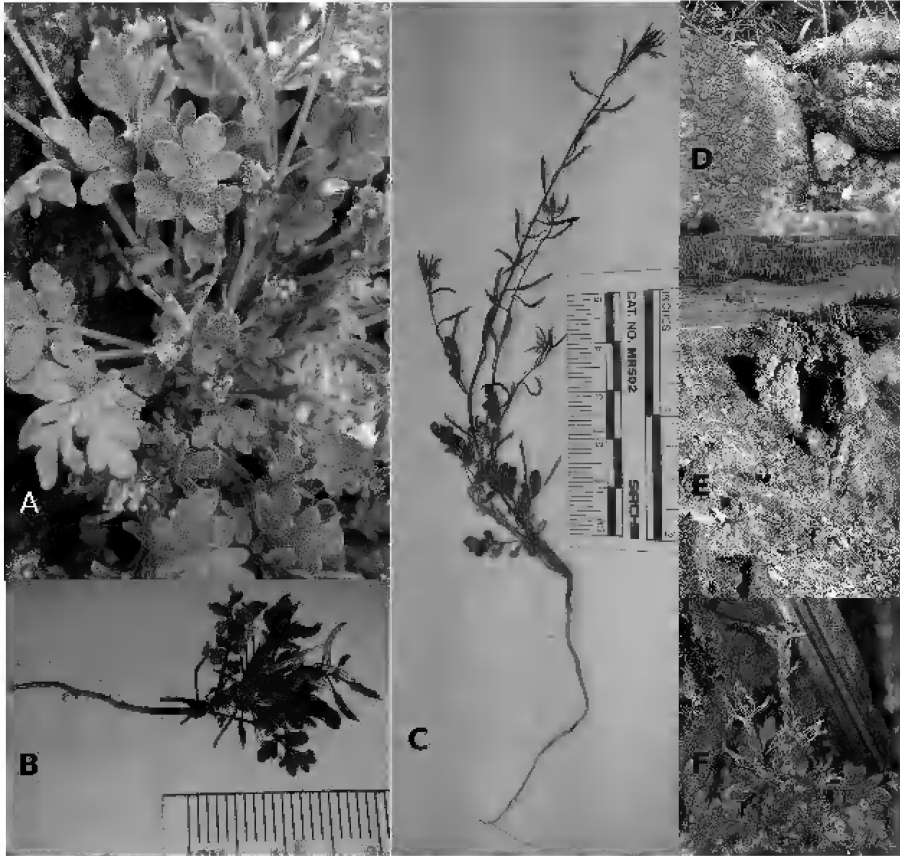
Figure 4. *Descurainia browniae* size, habit, and habitat. (A) large plant, (B) small plant, (C) large plant, (D) small plant and mammal feces, (E) habitat, and (F) small plant.

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LATHYRUS PALUSTRIS (FABACEAE) NEW TO ALABAMA

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ABSTRACT

Lathyrus palustris (Fabaceae) is reported new to the flora of Alabama based on a 2006 collection from the Ebenezer Swamp Ecological Preserve in Shelby County.

A study of the 235 specimens of *Lathyrus* deposited in the herbaria of Troy University (TROY), J.D. Freeman (AUA), The University of Alabama (UNA), The University of West Alabama (UWAL), Jacksonville State University (JSU), Anniston Museum of Natural History (AMAL), University of North Alabama (UNAF), Samford University (SAMF), and the Botanical Research Institute of Texas (BRIT) revealed a single collection of *L. palustris* L., which had been misidentified as *L. venosus* Muhl. ex Willd. *Lathyrus palustris* has not been included in Plant Life of Alabama (Mohr 1901), Annotated Checklist of the Vascular Plants of Alabama (Kral et al. 2011) or the Alabama Plant Atlas (Keener et al. 2017).

Voucher. **USA. Alabama.** Shelby Co.: W side of Ebenezer Swamp ca. 0.3 air mi E of State Route 119, ca. 0.35 air mi N of County Road 24, and ca. 5.0 air mi S of jct. of US Hwy 31 and State Route 119 in Alabaster, 33°9'56.24" N -86°48'44.62" W, 31 Aug. 2006, *Schotz 2037* (AMAL). Figures 1, 2.

Lathyrus palustris L., commonly known as Marsh Pea, has circumboreal distribution, occurring in both North America and Eurasia (Kavak 2014). In the USA, it is native throughout the northeastern and northcentral sections of the country and along the West Coast from Alaska to northern California. In the southeastern USA, it has been reported from Georgia, Kentucky, North Carolina and Tennessee (Kartesz 2015). Although the taxon appears to be globally secure (G5), it has been assigned a rank of S1 or S2 in eight states (NatureServe 2015). The closest reports of this taxon to the location in Shelby Co., Alabama, are Douglas Co., Georgia (210 km east), Dade Co., Georgia (255 km northeast), and Coffee Co., Tennessee (360 km north). In Georgia, *L. palustris* has a state rank of S1? (Georgia Department of Natural Resources 2017). The Tennessee Natural Heritage Program ranks this taxon as S1 with records from six counties (Coffee, Knox, Monroe, Rhea, Warren, and White) (Crabtree 2016). Unless additional populations are located in Alabama, it is expected this taxon will be listed as S1 (Critically Imperiled) by the Alabama Natural Heritage Program (2016).

Lathyrus palustris is classified as OBL (Obligate Wetland Taxon) (USDA, NRCS 2016) and is considered to be highly threatened by land-use conversion and habitat fragmentation (Southern Appalachian Species Viability Project 2002). Hopefully, this population will be safe since it occurs along the west side of The University of Montevallo's Ebenezer Swamp Ecological Preserve, an upland swamp on Spring Creek.
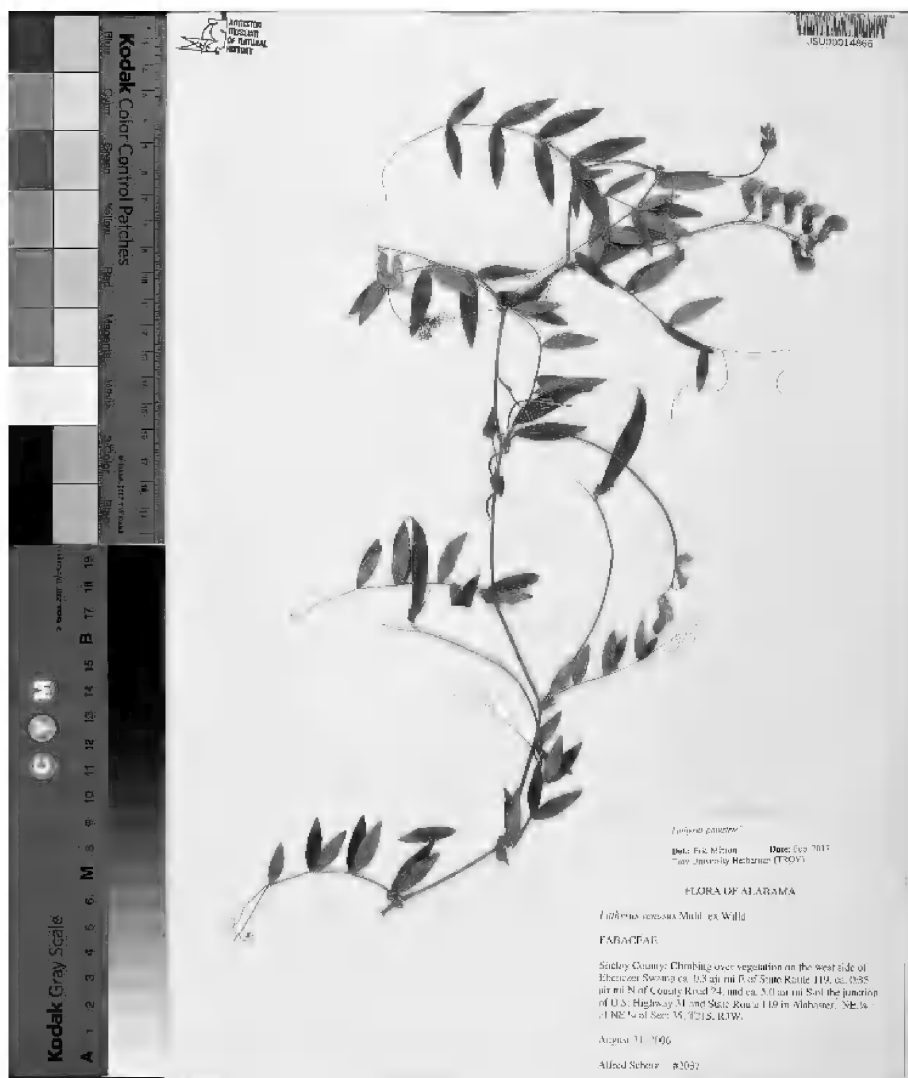
Figure 1. *Lathyrus palustris* from Shelby Co., Alabama (*Schotz 2037,* AMAL).

Figure 2. Map of Alabama showing distribution of *Lathyrus palustris* in Shelby County.

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DIPLACUS GRANITICOLA, SP. NOV. (PHRYMACEAE), FROM GRANITE CRACKS AND CREVICES IN THE CALIFORNIA SIERRA

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ABSTRACT

Diplacus graniticola Schoenig, **sp. nov.**, is segregated from *Diplacus layneae*. The new species is true in habitat to granite cracks and crevices in the California Sierra from Tuolumne Co. south through Mariposa, Madera, Fresno, and Tulare counties to Kern Co. and is partially sympatric with typical *D. layneae* in that area. Typical *D. layneae* occurs in various kinds of soil, including serpentine, and has a broader range in California. *Diplacus graniticola* is morphologically distinct from *D. layneae* in its shorter and more numerous nodes, vesture of longer hairs, calyces without white-membranous intercostal areas and broadly darkened ribs, and distinctive corolla markings. Further variation within *D. layneae* (after the exclusion of *D. graniticola*) remains to be clarified, especially in the North Coast Ranges.

Significant variation in the California endemic *Diplacus* (*Mimulus*) *layneae* (Greene) Nesom was noted by Thompson (2005, p. 120): "In the Yosemite National Park area (Tuolumne and Mariposa counties) and southward, *M. layneae* is differentiated into two forms that are known to co-occur ... . The first is a more elongate-pubescent form with a compact habit, growing almost exclusively from granite crevices. The second is a more puberulent form with an open habit, growing on granitic soils. The crevice-inhabiting form usually has more conspicuous radial markings on its spreading corolla limb and some yellow on the throat floor at the mouth. The form that occurs on soils has much more vague markings on its more weakly spreading corolla limb and a throat floor that is mostly white, washed with yellow only deep within the tube-throat, most resembling *M. layneae* from elsewhere in its range. The crevice-inhabiting form likely contains genes from *M. nanus* var. *mephiticus* [= *Diplacus mephiticus* (Greene) Nesom]."

Further field experience (Schoenig) confirms the distinction in habitat and morphology between these two expressions of *Diplacus layneae*. Thompson was not explicit regarding the evidence for his speculation about the genetic contribution from *D. mephiticus*, (although on specimen labels, he noted that the crevice-inhabiting form probably was a hybrid with *D. mephiticus*), but whatever their origin, the granite-crack plants have a coherent geographical range and are consistently distinct in morphology from typical *D. layneae* as well as other *Diplacus* species, even in areas of sympatry. They are recognized here as a distinct species.

DIPLACUS GRANITICOLA Schoenig, **sp. nov.** **TYPE: California**. Tuolumne Co.: N of Mather along Evergreen Road, Stanislaus National Forest-Yosemite National Park boundary, granite outcrops below road, 1400 m, growing only from granite crevices; common but local, hundreds of plants seen, 15 Jun 1988, *D.M. Thompson 953*, voucher for chromosome count of *n* = 8 (holotype: RSA, Figure 1; isotypes: JEPS!, OBI). Label data also include this: "Corolla magenta with 5 red-purple lines radiating from throat onto midveins of lobes and two red-purple

splotches at the 2 sinuses that separate the 2 upper from the 3 lower lobes; the 2 throat floor ridges yellow, at least partially bordered by red-purple. Red-purple markings may fuse partially. Probably a hybrid with *M. nanus* var. *mephiticus*."

Similar to *Diplacus layneae* in its dark-drying herbage, vestiture of gland-tipped hairs, flowers at all nodes and usually 2 per node, calyx strong ribbed and plicate, not inflated, corollas lavender to magenta, nearly regular to weakly bilabiate, and ciliate anthers; different from *D. layneae* in its (1) fidelity to cracks in granite, (2) flowering nodes 4–15(–20) in mature plants, distal internodes shorter than leaves, (3) vestiture of longer hairs, (4) calyces without white-membranous intercostal areas and broadly darkened ribs, and (5) distinctive and consistent corolla markings. See key couplet below for details.

Figure 1. *Diplacus graniticola*, holotype (rearranged for the illustration), RSA.

Herbs, annual, herbage usually drying distinctly darkened.   **Stems** erect, 6–12(–15) cm, villous with gland-tipped hairs 10–16 mm.   **Leaves** mostly cauline, relatively even-sized, 20–40 x 4–12 mm; petiole weakly delimited; blade mostly lanceolate to ovate-lanceolate, margins entire, rarely with a few shallow teeth distally, apex rounded to obtuse or acute, surfaces of proximal often glabrate and purplish abaxially, distal green, vesiture.   **Flowers** 2 per node, or 1 or 2 per node on a single plant, commonly at all nodes, chasmogamous.   **Fruiting pedicels** 1–3 mm.   **Calyces** 8–12 mm, not inflated in fruit, glandular-villous, ribs narrow, strongly raised, sometimes darkened, tube strongly plicate, intercostal areas green to purple, not membranous, lobes subequal, triangular, erect, lobe apex acute, not indurate.   **Corollas** nearly white or pale lavender to pinkish or pale to dark magenta, each lobe consistently with a dark medial line extending to near the lobe tip, throat with a dark red or purple splotch at the junction of each abaxial lobe and adjacent lateral lobe, throat floor sometimes with two adjacent white splotches at lateral lobe bases, palate ridges yellow, sparsely villous, tube-throat 15–20 mm, limb 10–16 mm wide, weakly bilabiate.   **Anthers** included, ciliate.   **Styles** glandular-puberulent; stigma included, lobes weakly unequal, abaxial 1.5 times as long as adaxial.   **Capsules** 6–10 mm.   **Chromosome number**, $2n = 16$ (*Thompson 889*, Fresno Co.; *Thompson 953*, Tuolumne Co.).   See Figures 3-13 for morphological and ecological contrasts with *D. layneae*.

Flowering Apr–Sep.   Granite cracks and crevices; 300–2134 m; Calif. (Fresno, Madera, Mariposa, Tulare [rare], and Tuolumne cos.).

Representative collections examined. California. <u>Fresno Co</u>. Dunlap, 1850 ft, 9 May 1954, *Barneby & Howell 11413* (CAS); along San Joaquin River at Kerckhoff Reservoir bridge, 1050 ft, 10 May 1954, *Barneby & Howell 11444* (CAS); 1 mi NW Auberry, Mariposa Quadrangle, 2300 ft, 5 Jun 1935, *Bullard 24* (UC); Huntington Lake, 6986 ft, 1 Jul 1926, *McDonald s.n.* (CAS); overlooking Big Sandy Valley (summit of small ridge on E face of mountain, property of (adjacent to) Ella Carter), Black Mountain, 2500 ft, 14 May 1955, *Bacigalupi et al. 5096* (JEPS); Jose Basin Sierra Natl Forest, San Joaquin River watershed, 3600 ft, 11 May 1959, *Bacigalupi et al. 7113* (JEPS); near road summit between Shaver Lake and Dinkey Creek, 5 Aug 1944, *Quick 68* (CAS); vicinity of Fence Meadow Lookout, Sierra Nevada, ca. 0.1 mi off W side of Forest Service Road 10S69 and 1.25 mi S of junction of Fence Meadow Lookout Road, 4300 ft, 8 Jul 1977, *Rubtzoff 9104* (CAS); Sequoia Natl Forest, 100 meters W of Hume Lake Rd. where USFS campground road forks off at Hume Lake, 5300 ft, 14 Jun 1998, *Schoenig 98* (UC); 1.7 road mi E of USFS Sugarloaf Road jct, along Auberry Road, 1.0 rd mi E of Meadow Lakes, 0.7 rd mi E of Alva Snow Road jct, 4428 ft, 19 Jul 1986, *Thompson 662* (JEPS, RSA); Huntington Lake, between and around Kinnikinnick and Catavee Campgrounds, 6986 ft, 20 Jul 1986, *Thompson 668* (RSA); 0.7 mi W Dunlap along Dunlap Road, 1820 ft, 12 May 1988, *Thompson 889* (JEPS, RSA); 0.5 mi S USFS Road 10S69 along USFS Hwy 9 (Hwy 7 on map), Haslett Basin, 2132 ft, 9 May 1992, *Thompson 1051* (JEPS, RSA); 1/4 mi E Auberry Mission Road (Jose Basin Road), 2000 ft, 13 May 1966, *Walker 66013* (JEPS 53963); above Trimmer Springs, 16 May 1937, *Winblad s.n.* (CAS); 0.4 mi W Dunlap (w slope of Sierra), Sierra Nevada, 1900 ft, 16 May 33, *Wolf 4751* (RSA, UC); ca. 40 km NE of Fresno (FSC), Sierra Natl Forest, 2.0 km NE of Tollhouse, Dry Creek drainage, top of Tollhouse Rock, 2935 ft, 1 Jun 1996, *York 784* (CAS); ca. 42 km NE of Fresno (FSC), 4.3 km NE of Tollhouse, Sierra Natl Forest, near end of Cripe Road, 3526 ft, 18 Apr 1997, *York 1714* (CAS); ca. 15 km NE of Fresno (FSC), Dry Creek basin, midslope on Owens Mountain, 754 ft, 29 May 1998, *York 2148* (CAS). <u>Madera Co.</u>: 2 mi W of Oakhurst, 2200 ft, 11 May 1954, *Barneby & Howell* 11451 (CAS); 2 mi S of Rd. 415 (on Rd. 400), 7 May 1960, *Broome & Olsen s.n.* (JEPS); Raymond, 9 May 1925, *Eastwood 12593* (CAS); along the 4 WD road between Little Shuteye Pass and Shuteye Peak Lookout, Chiquito Ridge, second switchback above saddle, 6900 ft, 2 Jul 1988, *Shevock 11848* (CAS 2 sheets). <u>Mariposa Co.</u>: Mormon Bar, 26 May 1895, *Congdon s.n.* (UC); due E of Silver Bar Rd. (0.3 mi from jct with Ben Hur-Mormon Bar Rd. between sources of Humbug and Mariposa Creeks), Greenamyers Hill, 2000 ft, 11 May 1980, *Hamon 80* (UC); Yosemite Natl Park, 4500 ft, no date, *Moncrief & Mowbray 74* (UC). <u>Tulare Co.</u>: N of Bear Creek (probably S of Badger near Adams Flat and Dry Creek), 1900 ft, 1 May 1896, *Purpus 1765* (UC). <u>Tuolumne Co.</u>: near Wapama Falls, Yosemite Natl Park, Hetch-Hetchy, 4050 ft, 17 May 1986, *Botti 267* (JEPS); Yosemite Natl Park, along the Hetch-Hetchy Trail, N side of Hetch-Hetchy Valley, 4050 ft, 16 May 1989, *Botti 314* (JEPS, RSA); road to Hetch Hetchy 2.8 mi NE of Mather, 5100 ft, 5 Aug 1980, *Ertter & Strachan 3938* (CAS); Hetch-

Hetchy, 3700 ft, 27 Jul 1909, *Jepson 3417* (JEPS); Mather, 4592 ft, 3 Jun 1931, *Keck 1205* (CAS); Mather, 4592 ft, 3 Jun 1931, *Keck 1206* (CAS, RSA); N of Hetch Hetchy, Sierra Nevada, Yosemite Natl Park, Miguel Meadows, 4050 ft, 21 Jul 1937, *Mason 11559* (UC); Stanislaus Natl Forest 0.2 mi W of Hetch Hetchy Rd, 1.0 mi NE of Mather (across from Natl Park Sign), 4921 ft, 24 May 1998, *Schoenig 98* (UC).
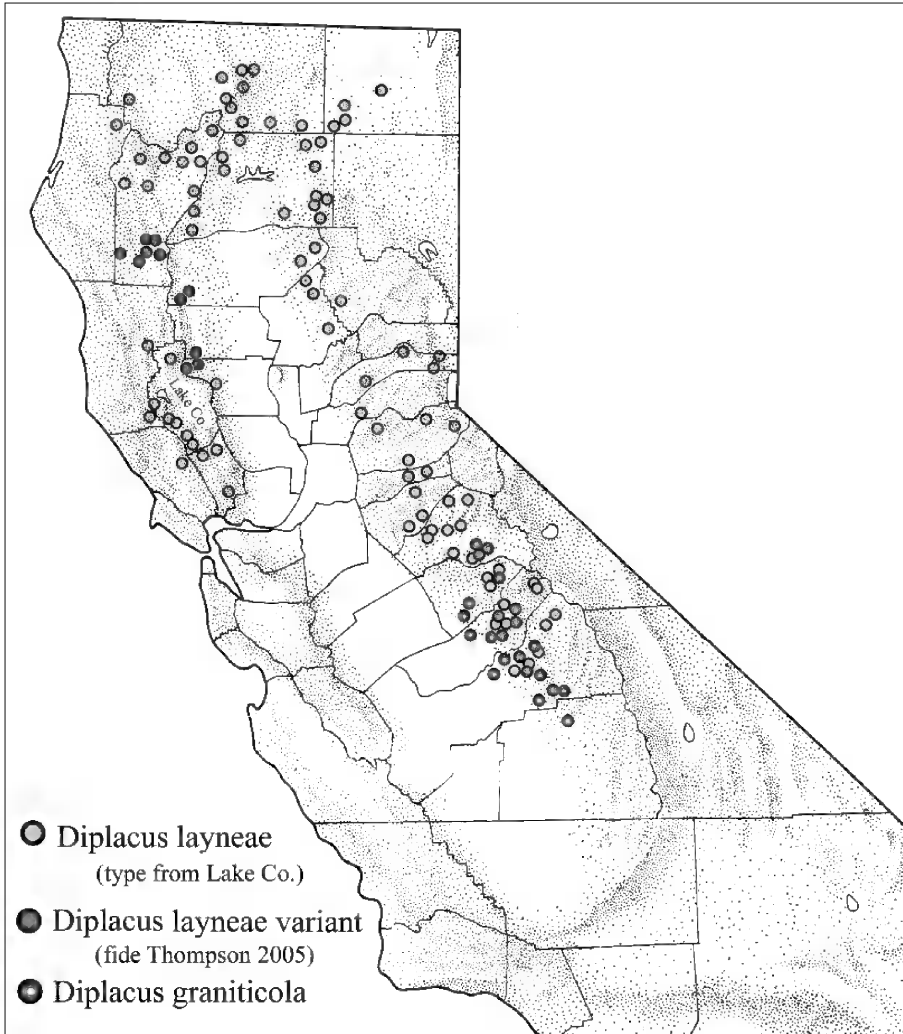

Figure 2. Distribution of *Diplacus graniticola*, typical *D. layneae*, and a variant of *D. layneae* hypothesized by Thompson (2005) to be a *D. layneae/D. nanus* hybrid. Distributions are drawn from published records from Thompson (2005), specimen records summarized in the California Consortium of Herbaria, and study of collections at UC-JEPS and CAS-DS. The type of *D. layneae* and its synonym, *D. brachiatus*, are from Lake County.

Diplacus graniticola occurs in the California Sierra from Tuolumne Co. south through Mariposa, Madera, and Fresno counties to Tulare Co.; it is partially sympatric with typical *D. layneae* in that area (Fig. 2). Exposed granite occurs in California both to the south and north of the range of *D. graniticola*, thus absence of substrate does not appear to limit its distribution. Where sympatric, *D. layneae* commonly occurs in granite-derived sand and gravel immediately adjacent to granite rock providing habitat for *D. graniticola*. Elsewhere in its range, *D. layneae* has been documented from soils from serpentine, metamorphic, and other types of volcanic rocks besides granite. Label data suggest that *D. graniticola* continues flowering later than sympatric *D. layneae*: Apr–Sep(–Oct) vs. Apr–Jul (–Aug).

Distinctions between *Diplacus graniticola* and *D. layneae* are summarized in the couplet below.

1. Plants compact in habit, nodes 4–15(–20), internodes shorter than the leaves; stem and leaf villous with gland-tipped hairs 1.0–1.6 mm long; calyx ribs narrowly darkened, intercostal areas green to purple, not membranous; corolla palate ridges yellow, each corolla lobe with a dark medial line extending to near the lobe tip; habitat primarily in granite cracks and crevices .... **Diplacus graniticola**

1. Plants open in habit, flowering nodes 3–6, internodes longer than the leaves; stem and leaf puberulent to pubescent with gland-tipped hairs 0.2–0.8 mm long; calyx ribs broadly darkened, intercostal areas whitish, membranous; corolla palate ridges white, each corolla lobe usually with a faint to dark medial line extending halfway or less to the lobe tip; habitat in serpentine, metamorphic, granitic, and other types of open volcanic soil, sand, and gravel .... **Diplacus layneae**

Variation in typical *Diplacus layneae*

Thompson (2005, p. 119) noted that "*Mimulus layneae* is one of the most complex and variable species in subg. *Schizoplacus*. It hybridizes with *M. nanus* in several parts of its geographic range and produces intermediates that detract from the otherwise distinctive concepts represented by each of these taxa. Fortunately, the problematic hybrid zones are limited in their size." Recognition of *Diplacus graniticola* as a distinct species significantly reduces the taxonomic complexity.

The major putative hybrid zone between *Diplacus layneae* and *D. nanus* (var. *nanus*) mapped and discussed by Thompson (his Figure 48, p. 117) is the region of southern Trinity Co., southwestern Tehama Co., and (perhaps slightly disjunct to) the vicinity of Snow Mountain on the Glenn/Colusa Co. line (see Fig. 2, here) –– the High North Coast Ranges. A collection series showing "all degrees of intermediacy" (fide Thompson, p. 120) was collected west of Paskenta, Tehama Co.: *Baker & Wagnon 12748* (nearest *M. layneae*), *12621* (center of variation), and *12676b* (nearest *M. nanus* var. *nanus*) –– the series is available at CAS, JEPS, and RSA. Thompson noted (p. 120) that "The two species have little altitudinal overlap in northwestern California, a factor that may limit the spread of the hybrids and some of the backcross progeny beyond these limited regions of sympatry." The current authors have not studied this situation.

There apparently are other small areas of overlap between *Diplacus layneae* and typical *D. nanus*, although the two are allopatric in most of northern California. Thompson, however, did not recognize (cite) putative hybrids from any other areas besides the one noted above.

Thompson (2003, 2005) regarded *Mimulus brachiatus* Penn. as a synonym of *Diplacus layneae* (both taxa are typified by collections from Lake Co.), but Pennell (1951) treated them as separate species, his key separating them primarily on the basis of smaller corollas with unequal lobes in *M. brachiatus* vs. larger corollas with nearly equal lobes in *M. layneae*. We agree with Thompson's assessment that both names represent the same entity. The type locality of *Mimulus brachiatus* is over serpentine substrate; the type of *Eunanus layneae* was collected on Bartlett Mountain, which apparently is without serpentine outcrops (LCAQMD 2016), thus *D. layneae* is tolerant of serpentine but not restricted to it.

Diplacus layneae (Greene) Nesom, Phytoneuron 2012-39: 29. 2012.   *Eunanus layneae* Greene, Bull. Calif. Acad. Sci. 1: 104. 1885.   *Mimulus layneae* (Greene) Jepson, Fl. W. Calif. (ed. 1), 405. 1901.   Lᴇᴄᴛᴏᴛʏᴘᴇ (Thompson 2005, p. 115): **California**. Lake Co.: Bartlett Mtn., 1884, *M.K. Curran s.n.* (BM digital image!; isolectotypes: F digital image!, UC [Katherine Brandegee as collector]!; probable isolectotype: GH digital image!).

Mimulus brachiatus Pennell, Notul. Nat. Acad. Nat. Sci. Philadelphia, No. 235: 2. 1951. Tʏᴘᴇ: **California**. Lake Co.: NE of Middletown, serpentine barrens, 1000 m, 19 Jun 1945, *H.D. Ripley & R.C. Barneby 6886* (holotype: PH digital image!).

ACKNOWLEDGEMENTS

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Figure 3. *Diplacus graniticola* (left) and *Diplacus layneae* (right) ventral view of corolla tube-throats showing color and pattern differences. These plants were 3 meters apart in granitic crevices and on adjacent scree respectively. Hetch-Hetchy area, Tuolumne Co. Photos © Steve Schoenig, May 2016.

Figure 4. *Diplacus graniticola.*   Eleven out of 18 nodes stripped of leaves and calyces showing the extremely close distal internode lengths in a mature plant. Hetch–Hetchy area. Photo © Steve Schoenig, September 2016.

Figure 5. *Diplacus graniticola*, Hetch–Hetchy, Tuolumne Co. Photo © Steve Schoenig, 1 July 1993.

Figure 6. *Diplacus graniticola*, Hume Lake, Fresno Co. Photo © Steve Schoenig, 2 June 2007.
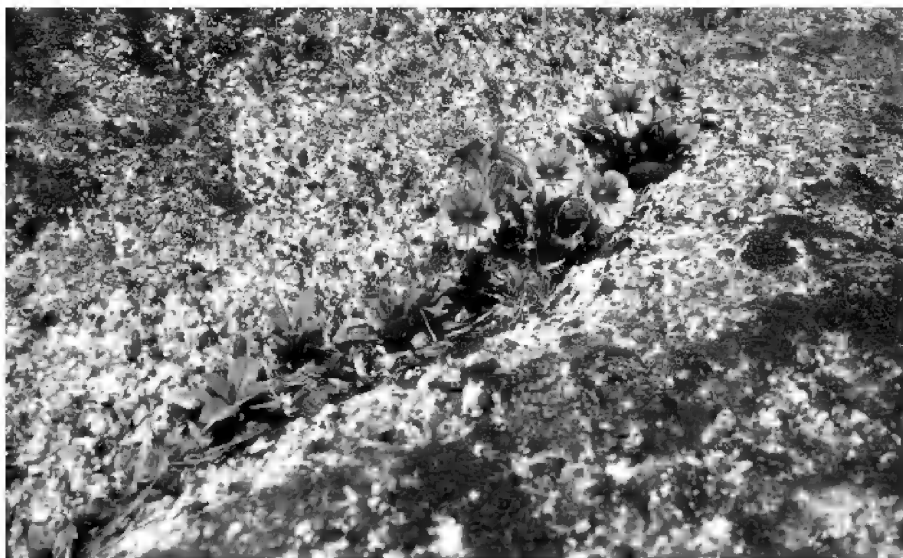
Figure 7. *Diplacus graniticola*, Hume Lake, Fresno Co. Photo © Neal Kramer, 2 June 2007.

Figure 8. *Diplacus graniticola*, San Joaquin River Gorge BLM Management Area, Fresno Co. Photo © Aaron Schusteff, 20 April 2013.

Figure 9. *Diplacus graniticola*, Yosemite National Park. Photo © Keir Morse, 15 July 2005.

Figure 10. *Diplacus graniticola*, Yosemite National Park. Photo © Keir Morse, 15 July 2005.

Figure 11. *Diplacus layneae* in gravelly soil immediately derived from granite, Yosemite National Park. Photo © Keir Morse, 12 July 2005.

Figure 12. *Diplacus layneae* in granite gravel, Yosemite Valley, Bridal Veil Fall Vista, Mariposa Co. Photo © Jean Pawek, 23 July 2011.

Figure 13. *Diplacus layneae* near Angwin, Napa Co. Photo © Steve Schoenig, May 1998.

TYPES OF SAGEBRUSH UPDATED
(*ARTEMISIA* SUBG. *TRIDENTATAE*, ASTERACEAE):
MISCELLANEOUS COMMENTS AND ADDITIONAL SPECIMENS FROM
THE BESSER AND TURCZANINOV MEMORIAL HERBARIA (KW)

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ABSTRACT
Corrections and additions are provided for the existing typifications of plant names in *Artemisia* subg. *Tridentatae*. In particular, second-step lectotypifications are proposed for the names *Artemisia trifida* Nutt., nom. illeg. (*A. tripartita* Rydb., the currently accepted replacement name), *A. fischeriana* Besser (= *A. californica* Lessing, the currently accepted name), and *A. pedatifida* Nutt. For several nomenclatural types of names listed in earlier publications as "holotypes," the type designations are corrected to lectotypes (Art. 9.9. of *ICN*). Newly discovered authentic specimens (mostly isolectotypes) of several names in the group are listed and discussed, mainly based on specimens deposited in the Besser and Turczaninov memorial herbaria at the National Herbarium of Ukraine (KW). The Turczaninov herbarium is particularly rich in Nuttall's specimens, which are often better represented and better preserved than corresponding specimens available from BM, GH, K, PH, and some other major herbaria.

Artemisia L. subg. *Tridentatae* (Rydb.) McArthur (Asteraceae), containing sagebrush species, is a morphologically, geographically and phylogenetically well outlined group restricted exclusively (or mainly?) to North America, which was recently treated taxonomically by Shultz (2006b, 2009). Recent molecular phylogenetic studies confirmed a rather isolated position of the group within the genus (Kornkven et al. 1998, 1999; Torrell et al. 1999; Watson et al. 2002; Vallès et al. 2003; Sanz et al. 2008; Garcia et al. 2011a) but also demonstrated that it is phylogenetically rooted in *Artemisia* subg. *Artemisia* in its current rather wide circumscription. It was also confirmed (Vallès et al. 2003; Sanz et al. 2008; Garcia et al. 2011a) that the previously recognized genera *Picrothamnus* Nutt. and *Sphaeromeria* Nutt. (see Nuttall 1841; Holmgren et al. 1976; Cronquist 1994; Shultz 2006a, 2006b; Lowrey & Shultz 2006 etc.) should be included in it. New nomenclatural combinations in *Artemisia* have been already proposed for the majority of taxa earlier included in *Sphaeromeria* (Garcia et al. 2011b). Since the "*A. tridentata* clade" is phylogenetically sister to *Artemisia* subg. *Artemisia* sect. *Artemisia* sensu lato, the sectional rank for "sagebrushes" is probably justified, or, alternatively, some other clades should be recognized as subgenera, if the subgeneric rank is retained for the "*A. tridentata* clade." Further changes in infrageneric taxonomy of the genus seem to be inevitable.

However, pending further research, for convenience here we refer to that group as "subg. *Tridentatae*," in the circumscription accepted by Shultz (2006b, 2009), with addition of some taxa, as suggested by Garcia et al. (2011b).

The data on types of names of most taxa of that subgenus (in its traditional circumscription) were summarized by Shultz (2009), and earlier by Cronquist (1994). However, for some names, corrections and sometimes second-step lectotypifications were needed.

In the course of the preparation of the present note we consulted the available databases of scanned herbarium specimens (mainly JSTOR Global Plants 2017–onward) and, most importantly, the vast collections of historical herbarium specimens of *Artemisia* deposited in the memorial herbaria of Besser and Turczaninov in the National Herbarium of Ukraine (KW, Herbarium of the M.G. Kholodny Institute of Botany, National Academy of Sciences of Ukraine; here and below the herbarium acronyms are given following Thiers 2017–onward).

Willibald [in some sources Wilibald] Swibert Joseph Gottlieb von Besser (1784–1842; in Russian sometimes mentioned as Виллибальд Готтлибович Бессер), an Austrian-born botanist who worked mainly in Kremenets and Kiev (formerly the Russian Empire, now Ukraine), was one of early monographers of *Artemisia* who published several important contributions on taxonomy of the genus (Besser 1829, 1832, 1834a, 1834b, 1835) and also contributed to the treatment of *Artemisia* in de Candolle's *Prodromus…* (Candolle "1837," published 1838). Many of his taxa are still widely recognized in standard floras and manuals (Poljakov 1961; Korobkov 1992; Krasnoborov 1997; Ling et al. 2011; Shultz 2006b etc.; see also IPNI 2017–onward). Nikolai (Nicolai or Nicholas) Stepanovich Turczaninov (1796–1863; Николай Степанович Турчанинов in Russian; also sometimes transliterated as Turczaninow, Turchaninov, Turtschaninow, or Turtschaninoff) was a devoted plant collector and taxonomist who exchanged plant specimens with many contemporary botanists and accumulated a large herbarium of more than 150 000 specimens (probably much more than 170 000 specimens, if we consider specimens placed on the same sheet or in the same folder/envelope). Main collections of these two botanists are deposited in KW as two memorial herbaria kept separately from other KW collections, while their duplicate specimens are also available from many other herbaria (Jain 1970; Stafleu & Cowan 1976, 1986; Myakushko 1976; Marchant 1990; Krytzka & Mosyakin 2002; Shiyan 2011 etc.).

Both these historical collections are amazingly rich in types from all parts of the world; many types (especially those of taxa described by Turczaninov himself) have been already identified, scanned and databased (see JSTOR Global Plants 2017–onward), but many other type specimens still remain in these general collections, awaiting proper identification and further research. In particular, the Turczaninov herbarium contains numerous North American specimens collected by Thomas Nuttall (1786–1859), but complete inventory of these specimens has not been done yet. Nuttall's original collections are mainly deposited in BM and PH, with additional specimens or duplicates in GH, K, MO, NY, OXF, and some other herbaria (see Stafleu & Cowan 1981).

Type specimens of *Artemisia* subg. *Tridentatae*: corrections and second-step lectotypifications
The taxa are listed below following the treatment by Shultz (2009). If necessary, notes on their corrected typification are provided.

ARTEMISIA CANA Pursh, Fl. Amer. Sept. 2: 521. 1814. *Seriphidium canum* (Pursh) W.A. Weber, Phytologia 55: 7. 1984. **TYPE**: According to the protologue: "On the Missouri. *M. Lewis.* Aug.–Oct. *v. s. in herb. Lewis.*" As cited by Shultz (2009: 37): "U.S.A.: "on the bluffs of the Missouri River," *M. Lewis 60* (lectotype, here designated: PH-LC 19)." **LECTOTYPE**: PH-LC 19 (PH00043165), designated by Cronquist (1994), corrected and verified by Reveal et al.

(1999), and accepted by Shultz (2009); image available from JSTOR Global Plants (2017–onward).

Artemisia columbiensis Nutt., Gen. N. Amer. Pl. 2: 142. 1818. **TYPE**: According to the protologue (Nuttall 1818: 142): "On the arid and saline hills which border the Missouri and the lesser streams, commencing about 30 miles below White River; and continuing to the Mountains (or Northern Andes), it occurs still more abundantly on the barren plains of the Columbia river <…>. It is the plant which was known to the party of Lewis and Clarke by the name of "Wild Sage," and appears to be *A. cana* of Pursh. Fl. Am. 2. p. 521." As cited by Shultz (2009: 38): "U.S.A.: "on arid & saline hills that border the Missouri & lesser streams, commencing ca. 30 miles below the White River (plant called 'wild sage' by Lewis & Clark)," [1811], *T. Nuttall s.n.* (holotype: PH!)." **LECTOTYPE**: *Nuttall, s.n.* PH00008343, designated by Shultz (2009, as "holotype"); image available from JSTOR Global Plants (2017–onward).

In her treatment Shultz (2009: 37) cited as the type of *Artemisia cana* the specimen "*Lewis 60* (lectotype, here designated: PH-LC 19!)". In fact, the lectotype was designated by Cronquist (1994: 162) who, however, cited it as the "holotype" (an error correctable under Art. 9.9 of *ICN*: McNeill et al. 2012), and with a wrong collection number (6 instead of 60, evidently a technical error). These errors were corrected by Reveal et al. (1999: 10), who properly termed this specimen as the lectotype and commented that it was collected "near the mouth of the Cheyenne River in Stanley Co., South Dakota". Several historical collections of *A. cana* in the memorial herbaria of Besser and Turczaninov (KW) do not represent original material used by Pursh (1814).

In his protologue of *A. columbiensis*, Nuttall (1818) cited numerous localities in the western part of the USA (see above). Any specimens (known or still unidentified) collected and identified by Nuttall and matching these localities are technically syntypes. Since Nuttall did not indicate (directly or indirectly) any specimen as the type and we cannot exclude the existence of additional specimens (syntypes), the specimen PH00008343 should be treated as the lectotype designated by Shultz (2009). No authentic specimens identified as *A. columbiensis* were found at KW.

ARTEMISIA TRIPARTITA Rydb., Mem. New York Bot. Gard. 1: 432. 1900. *Seriphidium tripartitum* (Rydb.) W.A. Weber, Phytologia 55: 8. 1984. *Artemisia trifida* Nutt., Trans. Amer. Philos. Soc., n. s., 7: 398. 1841, *nom illeg.*, *non* Turcz. 1832. *Artemisia tridentata* Nutt. subsp. *trifida* H.M. Hall & Clements, Publ. Carnegie Inst. Wash. 326: 137. 1923. *Artemisia tridentata* Nutt. var. *trifida* (H.M. Hall & Clements) McMinn, Man. Calif. Shrubs: 608. 1939. **TYPE**: According to the protologue (Nuttall 1841: 398): "Plains of the Rocky Mountains and Oregon." As cited by Shultz (2009: 46): "Plains of the Rocky Mts.," [probably Idaho, 1834], *T. Nuttall s.n* (holotype: BM!; isotypes: PH!, GH!)." **LECTOTYPE** (here designated, second-step lectotypification): Plains of the Columbia & R. Mts., *Nuttall s.n.* BM000810854, image available from JSTOR Global Plants (2017–onward); isolectotypes: GH00002743, KW001002845 and KW001002846 (Figure 1), PH00025116.

Artemisia tripartita is the replacement name proposed by Rydberg (1900) instead of the illegitimate name *A. trifida* Nutt. (Nuttall 1841). Consequently (Art. 7.4 of *ICN*: McNeill et al. 2012), it has the same type as the replaced name. Both Cronquist (1994) and Shultz (2009) cited Nuttall's specimen from BM as the "holotype". However, in the protologue there is no indication of any particular specimen as the type. Thus, all specimens of the same origin deposited in various herbaria are technically syntypes, and the selection of a lectotype was necessary. The designation of the specimen from BM as the "holotype" should be thus corrected to the lectotype (Art. 9.9 of *ICN*: McNeill et al. 2012). However, there are three specimens (BM000810853, BM000810854, BM000810855) mounted on the same sheet in BM, and two of them (BM000810854 and BM000810855) were collected by Nuttall and belong to original material of *A. trifida* (and

BM000810855 belongs to Nuttal's variety "β *rigida*", see below). Consequently, Cronquist (1994) and Shultz (2009) did the first-step lectotypification. Here we propose the second-step lectotypification and designate the specimen BM000810854 ("Plains of the Columbia & R. Mts." collected by Nuttall) as the lectotype.

The specimens from PH, GH, and the newly discovered duplicates from KW (see below) can be thus treated as isolectotypes. There are two Nuttall's specimen in the Turczaninov herbarium at KW: "*Art. trifida* Nutt. Nuttall. R. Mts." (KW001002846) and "*Artemisia trifida*. Oregon. R. Mts." (KW001002845; handwriting by Nuttall), both on the same sheet with KW001002847 ("*Artemisia trifida* β. *rigida*", see below) (Figure 1). These specimens are represented by plant fragments (probably parts of more complete specimens?), provided to Turczaninov either directly by Nuttall or by some other person.

The name *Artemisia tridentata* subsp. *trifida* H.M. Hall & Clements (1923) is sometimes cited with the authorship "(Nutt.) H.M. Hall & Clements" (see, for example, Shultz 2009: 46). However, since the name *A. trifida* Nutt. is illegitimate, the subspecies name should be treated as a new replacement name authored by Hall & Clements, with the same type as the illegitimate species name (Art. 58.1 of *ICN*: McNeill et al. 2012). The authorship of the variety, *A. tridentata* var. *trifida*, should be thus cited as "(H.M. Hall & Clements) McMinn".

ARTEMISIA RIGIDA (Nutt.) A. Gray, Proc. Amer. Acad. Arts 19: 49. 1883. *Artemisia trifida* Nutt. var. *rigida* Nutt., Trans. Amer. Philos. Soc., n. s., 7: 398. 1841. *Seriphidium rigidum* (Nutt.) W.A. Weber, Phytologia 55: 8. 1984. TYPE: According to the protologue (Nuttall 1841: 398): "From the plains of Lewis' River, in the Rocky Mountains, I have a variety, β. *rigida*, in which the leaves are shining and silky, rigidly three-forked and acute, but of this I have no flowers. It is, perhaps, a distinct species." As cited by Shultz (2009: 51): "U.S.A. [presumably Washington]: "plains of the Lewis [Snake] River" [presumably 1834], *T. Nuttall s.n.* (holotype: BM!; isotype: PH!)." LECTOTYPE: Lewis River, *Nuttall s.n.*, BM000810855, designated by Cronquist (1994, as "holotype") and verified by Shultz (2009, as "holotype"); image available from JSTOR Global Plants (2017–onward); isolectotypes: BM000810855 (?), GH00002743, KW001002847 (?) (Figure 1), PH00025116.

The specimen from BM listed by Cronquist (1994) and Shultz (2009) as the "holotype" is in fact the lectotype (Art. 9.9 of *ICN*: McNeill et al. 2012). Additional specimens are available from PH (PH00025116) and GH (GH00002743), both verified by Shultz as "isotypes" (in fact, isolectotypes) of *A. trifida* var. *rigida* (see JSTOR Global Plants 2017–onward). A specimen "*Artemisia trifida* β *rigida*. R. Mts. [Rocky Mountains]. Nuttall" recently found in the Turczaninov herbarium (KW KW001002847; Figure 1) is also most probably an isolectotype.

ARTEMISIA ARBUSCULA Nutt., Trans. Amer. Philos. Soc., n. s., 7: 398. 1841. *Seriphidium arbusculum* (Nutt.) W.A. Weber, Phytologia 55: 7. 1984. TYPE: According to the protologue (Nuttall 1841: 398): "On the arid plains of Upper California, on Lewis' River." As cited by Shultz (2009: 54): "U.S.A., [presumably Washington]: "arid plains of the Lewis [Snake] River" [presumably 1834], *T. Nuttall s.n.* (holotype: BM!; isotypes: PH!, GH!, K!)." LECTOTYPE: BM001025660, designated by Cronquist (1994, as "holotype") and verified by Shultz (2009, as "holotype"); image available from JSTOR Global Plants (2017–onward); isolectotypes: GH00002691, K000942175, KW001002848 (?) (Figure 2), KW001002849 (Figure 2), PH00025095.

As with some other type designations discussed above, the "holotype" cited by Cronquist (1994: 160) and Shultz (2009: 54) is in fact the lectotype, and the specimens from PH (PH00025095),

GH (GH00002691) and K (K000942175) mentioned by Shultz (2009) are thus isolectotypes (images available from JSTOR Global Plants 2017–onward). Two additional authentic specimens were found in the Turczaninov collection at KW: "*Artemisia arbuscula*. Nuttall. R. Mts." (KW001002848) and "*Artemisia arbuscula* Nutt. Nuttall. Lewis River. U. Cal. [Upper California]" (KW001002849) (Figure 2). At least the second specimen from KW can be reliably considered an isolectotype.

ARTEMISIA TRIDENTATA Nutt., Trans. Amer. Philos. Soc., n. s., 7: 398. 1841. *Seriphidium tridentatum* (Nutt.) W.A. Weber, Phytologia 55: 8. 1984. **TYPE:** According to the protologue (Nuttall 1841: 398): "Plains of the Oregon, and Lewis' River." As cited by Shultz (2009: 75): "U.S.A.: "plains of the Columbia River" [probably in Oregon or Washington, 1834 or 1835], *T. Nuttall s.n.* (lectotype, designated by Cronquist, 1994: PH!)." **LECTOTYPE** (designated by Schultz 2009: 75): PH00004399, see below; image available from JSTOR Global Plants (2017–onward); isolectotypes: BM001025663, GH00002740, KW001002841 (Figure 3).

Shultz (2009: 75) listed the specimen from PH as the lectotype designated by Cronquist (1994: 158). However, when considering the type of *Artemisia tridentata*, Cronquist (1994: 158) mentioned two specimens ("*Nuttall*, plains of the Oregon; represented at BM!, PH!") and commented that "[t]he PH specimen is clearly the variety to which the name has traditionally been applied; the BM specimen is ambiguous and might belong to the phase here called var. *wyomingensis*." Since Cronquist did not **explicitly** indicate a specimen from either PH (PH00004399) or BM (BM001025663) as the type (lectotype), in our opinion, effective lectotypification of the name has been done by Shultz (2009). The image of an additional isolectotype (GH00002740) is available online (JSTOR Global Plants 2017–onward). There is one additional authentic Nuttall's specimen of *A. tridentata* in the Turczaninov collection at KW: "*Artemisia tridentata* Nuttall. Oregon. R. Mts. [Rocky Mountains]. Nuttall" (KW001002841), which can be treated as an isolectotype (Figure 3).

ARTEMISIA CALIFORNICA Lessing, Linnaea 6: 523. 1831. *Crossostephium californicum* (Lessing) Rydb., N. Amer. Fl. 34(3): 243. 1914. **TYPE:** According to the protologue (Lessing 1831: 523): "Ill. de Chamisso in California (v. sp. s. ∞)." As cited by Shultz (2009: 97): "U.S.A. California: San Francisco [1816], *Chamisso s.n.* (holotype: HAL!; isotypes: GH!)." **LECTOTYPE:** HAL0105121, designated by Shultz (2009, as "holotype"; see below); image available from JSTOR Global Plants (2017–onward); isolectotypes: GH00002698, KW001000941 (Figure 4), LE00018144.

Artemisia fischeriana Besser, Tent. Abrotanis: 21. 1832 (preprint from Nouv. Mém. Soc. Imp. Naturalistes Moscou); Besser, Nouv. Mém. Soc. Imp. Naturalistes Moscou 3: 21. 1834. **TYPE:** According to the protologue (Besser 1832: 21): "Ad sinum S. Francisci Californiæ in planitie, unde ab amicissimo Eschscholtzio: prætera in herbarii clarissimi Fischeri Directoris horti botanici Imperatorii Petropolitani etc et D^ris Fleischeri (v. sp. s.)." As cited by Shultz (2009: 97): "U.S.A. California: San Francisco Bay, *Eschscholtz s.n.* (holotype: KW!)." **LECTOTYPE** (here designated, second-step lectotypification; see below): KW001000943 (Figure 5); isolectotypes: KW001000942 (Figure 6), KW001000938 (Figure 7).

Artemisia foliosa Nutt., Trans. Amer. Philos. Soc., n. s., 7: 397. 1841. *Crossostephium foliosum* (Nutt.) Rydb., N. Amer. Fl. 34(3): 243. 1914. **TYPE:** According to the protologue (Nuttall 1841: 397): "Common round Monterrey, in Upper California." As cited by Shultz (2009: 97): "U.S.A. California: Monterey [1834], *T. Nuttall s.n.* (holotype: PH!)." **LECTOTYPE:** PH00025097, designated by Shultz (2009, as "holotype"); image available from JSTOR Global Plants (2017–onward); isolectotypes: GH00002701 (?), KW001002842 (Figure 8).

Artemisia abrotanoides Nutt., Trans. Amer. Philos. Soc., n. s., 7: 399. 1841, *nom. illeg., non* Jacq. ex DC. 1838. — **TYPE:** According to the protologue (Nuttall 1841: 399): "Near St. Barbara, Upper California." As cited by Shultz (2009: 97): "U.S.A. California: near Santa Barbara,

[1836], *T. Nuttall s.n.* (holotype: BM!)." Probable **HOLOTYPE**: BM, digital image not traced (assuming there is only one original specimen; Art. 9.1 of *ICN*).

Both Cronquist (1994) and Shultz (2009) listed a specimen from HAL as the "holotype" of *Artemisia californica*. However, since several collections of Ludolf Karl Adelbert von Chamisso (1781–1838) made at San Francisco Bay exist in several herbaria (GH00002698, LE00018144 – listed in the JSTOR Global Plants database as "San Tranurco", which is evidently a misspelling of San Francisco, etc.), the HAL specimen (HAL0105121) should be regarded the lectotype (Art. 9.9 of *ICN*: McNeill et al. 2012). There is one additional specimen in the Besser herbarium at KW, which is also an isolectotype: "*Artemisia californica* Lessing. San Francisco Californiae. A. Chamisso. E Herb. reg. Berol. 40" (KW001000941). The provenance note ("E Herb. reg. Berol. 40") indicates that the specimen was received by Besser in 1840 from the Berlin herbarium (now B); it was Besser's usual practice to indicate the origin of his specimens in that way (see Mosyakin et al. 2017). An additional curatorial label with the typographically printed heading "Herbarium Universitatis S^ti Vladimiri" (Herbarium of St. Vladimir University of Kiev) has the handwritten inscription "Herbarium Besseri". The specimen BM001025667 listed in the online database (JSTOR Global Plants 2017–onward) as the "type of *Artemisia californica*" was collected by Nuttall and thus is not part of the original material.

Shultz (2009) listed a specimen from KW as the "holotype" of *Artemisia fischeriana* Besser. However, in the Besser collection at KW there are several original specimens (mounted on three sheets) collected by Johann Friedrich Gustav von Eschscholtz (1793–1831) and his co-collector (see below) in San Francisco Bay and annotated by Besser as *A. fischeriana*. Consequently, the second-step lectotypification was needed. Thus, we designate here the specimen KW001000943 as the lectotype (Figure 5). This specimen consists of two plant fragments (both most probably representing parts of the same plant, or definitely parts of the same collection) and has the small label "Californien" with an additional inscription by Besser "Esch. 31", where "Esch." means Eschscholtz and "31" is the year (1831) of provenance. There are two additional labels, one with a complete handwritten description of the new taxon made by Besser, with the name "*Fischeriana*" and the geographical origin ("Ad Sin. S. Francisci Californ. Esch. Hbr. Fisch.") written on the top. "Hbr. Fisch." indicates that the specimen has been received by Besser from Fischer's herbarium. Since the species epithet commemorates the German-born Russian botanist Friedrich Ernst Ludwig von Fischer (1782–1854; also known in Russian as Фёдор Богданович Фишер), it is an additional argument in favor of selecting this specimen as the lectotype. A small envelope with loose fragments of inflorescences glued in the lower right part of the sheet has the name "*Artemisia. A. californica*" written by some unidentified person.

The second specimen (KW001000942, Figure 6) is represented by a rather large terminal fertile branch, with the original label in German: "Bei Californien, [one word illegible; probably "basin"?] Port St. Francisco. Esch. 1831". The provenance note ("Esch. 1831") added by Besser indicates that the plant was collected or provided by Eschscholtz and received by Besser in 1831.

Another sheet has two specimens (Figure 7). The first one (KW001000939) is represented by a terminal branch and has the label "*Artemisia Fischeriana* mihi. S^t. Francisco. Hb. Acad. Imp. Sc. Choris". This specimen was collected by Louis (also Ludovik or Ludwig) Choris (1795–1828), a German-Ukrainian painter and explorer, a co-collector of Eschscholtz and Chamisso, who also participated in the expedition onboard the ship *Rurik* (also *Rurick* or *Ryurik*; *Рюрик* in Russian) during 1815–1818 under the command of Otto von Kotzebue and spent October 1816 in San Francisco Bay (Kotzebue 1821; Choris 1822, 1913). The specimen was received by Besser from the herbarium of the Imperial Academy of Sciences in St. Petersburg (now mainly part of LE). The second specimen (KW001000938, on the same sheet with KW001000939) has two fragments of terminal branches and the label "Remittenda. Ad Sinum S. Francisci Californiae. Eschscholtz". The

two cited specimens (KW001000942 and KW001000938) collected by Eschscholtz in San Francisco can be considered isolectotypes. Some additional isolectotypes can be expected in other German and Russian herbaria.

When preparing his treatment, Besser (1832, 1834) probably was unaware of the new species *Artemisia californica* already described by Lessing (1831) just one year before, and thus he published his description of the new species *A. fischeriana*, which is in fact conspecific with *A. californica*. As discussed earlier (Mosyakin et al. 2017), the preprint (Besser 1832) of Besser's treatment (Besser 1834a) was published already in 1832, only shortly after the publication of the work by Lessing.

The specimen from PH (PH00025097) listed by Shultz (2009) as the "holotype" of *Artemisia foliosa* Nutt. should be considered the lectotype (Art. 9.9 of *ICN*: McNeill et al. 2012) because of the existence of several other original specimens (syntypes). In particular, we found in the Turczaninov collection at KW an additional isolectotype with the following label: "*Artemisia *foliosa*. Monterrey. U. California. Nuttall" (KW001002842, Figure 8). This specimen has an additional label, "Artemisias. R. Mts. Nuttall," which was probably originally supplied by Nuttall with several other specimens or their fragments. A specimen from GH with the label "Monterrey" (GH00002701) is most probably also a fragment of some other original specimen (isolectotype?).

No authentic specimens annotated as *Artemisia abrotanoides* have been found at KW.

Some taxa not treated by Shultz (2009) but now included in *Artemisia* subg. *Tridentatae*

As mentioned above, molecular phylogenetic studies (see Garcia et al. 2011a, 2011b and references therein) demonstrated that several additional species of *Artemisia* and all species earlier placed of *Sphaeromeria* and *Picrothamnus* should be included in *Artemisia* subg. *Tridentatae*. We found in the Turczaninov herbarium at KW several authentic specimens of *A. pedatifida* Nutt., *Sphaeromeria argentea* Nutt., and *S. capitata* Nutt. collected and annotated by Nuttall. These taxa were not included in the taxonomic monograph by Shultz (2009). Nomenclatural notes on *A. pedatifida* are provided below.

ARTEMISIA PEDATIFIDA Nutt., Trans. Amer. Philos. Soc., n. s., 7: 399. 1841. TYPE: According to the protologue (Nuttall 1841: 399): "Arid plains of Lewis' River, Rocky Mountains." As cited by Shultz (2009: 110): "U.S.A. Idaho: "arid plains of Lewis [Snake] River," *T. Nuttall s.n.* (holotype: GH!)." LECTOTYPE (here designated, second-step lectotypification, see below): Arid plains of Lewis' River, *Nuttall, s.n.* GH00002722,; image available from JSTOR Global Plants (2017–onward); isolectotypes: GH00002723, K000942263, KW001002850 and KW001002851 (Figure 9), PH00004387.

Shultz (2009: 29) preferred to keep this species in *Artemisia* subg. *Dracunculus* Besser but listed it among "Excluded species" and provided the type information (see above). However, there are at least two original specimens in GH and several more in other herbaria, and thus the designation of a "holotype" by Shultz (2009) can be regarded as a first-step lectotypification. The second-step lectotypification is proposed here. Images of additional specimens (isolectotypes) from GH, K, and PH are available from JSTOR Global Plants (2017–onward).

We found in the Turczaninov herbarium at KW two additional specimens (isolectotypes, on the same sheet) collected by Nuttall: "*Artemisia pedatifida*. Nuttall. R. Mts." (KW001002851) and "*Artemisia pedatifida*. Lewis River [handwriting by Nuttall]" (KW001002850) (Figure 9).

Nuttall's species earlier placed in *Sphaeromeria* and now transferred to *Artemisia* will be discussed in detail in a separate article.

Conclusions

Our analysis of the existing type designations of selected names of taxa now placed in *Artemisia* subg. *Tridentatae* resulted in several corrections (mostly according to Art. 9.9 of *ICN*: McNeill et al. 2012) and second-step lectotypifications. Additional authentic specimens collected by Nuttall, Eschscholtz, and Chamisso (taxa described by Nuttall, Besser, and Lessing, respectively) have been identified in the National Herbarium of Ukraine, KW (Besser and Turczaninov memorial collections).

Finally, we would like to draw attention of researchers working on taxa described by Nuttall, as well as those interested in the history of early botanical exploration of North America, to numerous Nuttall's herbarium specimens deposited in the Turczaninov memorial herbarium at KW. Amazingly, some specimens from KW are even better represented and better preserved than corresponding specimens available from such herbaria as BM, GH, K, PH, etc. In some cases these additional KW specimens can be very useful for establishing the true identity of some taxa. For example, Mosyakin (1995, 2003) was able to restore the neglected name *Corispermum americanum* (Nutt.) Nutt. (Chenopodiaceae) after studying a few fruits (crucially important for identification of *Corispermum* species) available on the isolectotype of this species at KW, while no fruits were available from the lectotype at PH.

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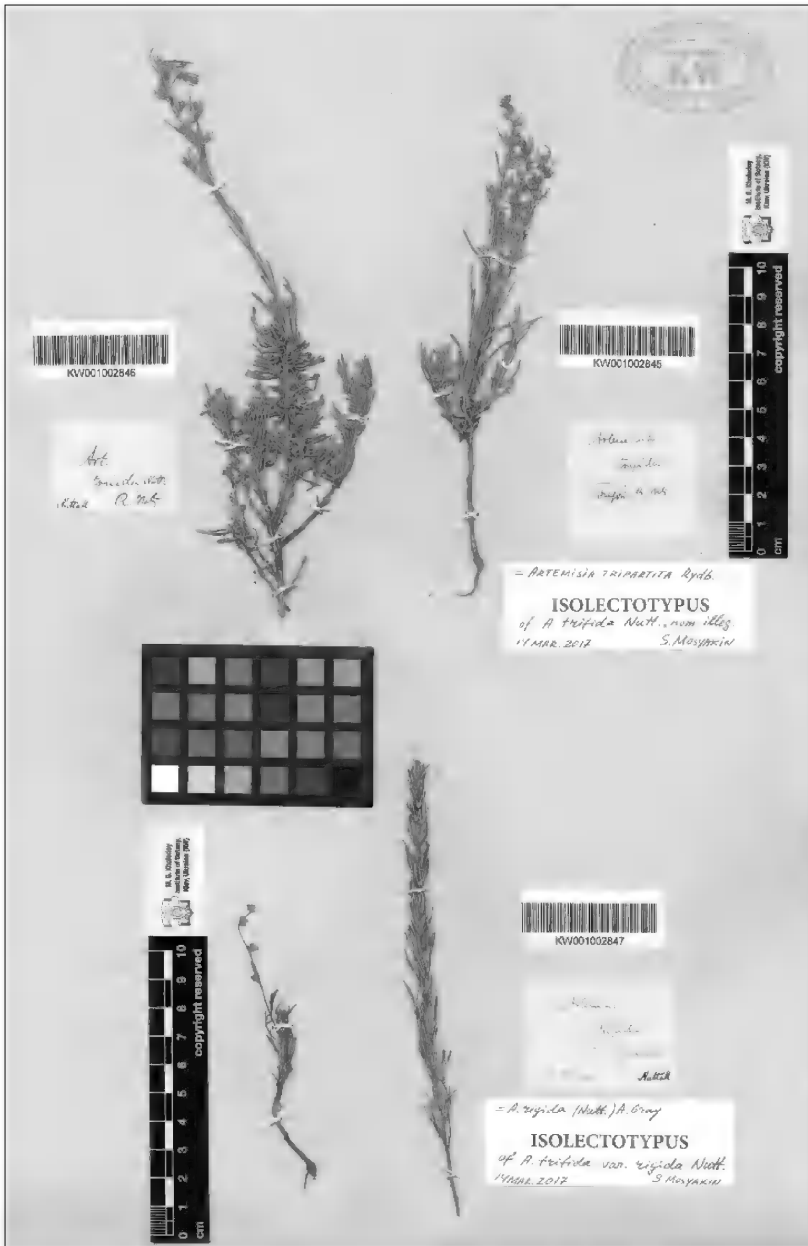
Figure 1. Isolectotypes of *Artemisia trifida* Nutt. (KW001002845, upper right; KW001002846, upper left) and possible isolectotype of *A. trifida* var. *rigida* Nutt. (KW001002847, bottom).
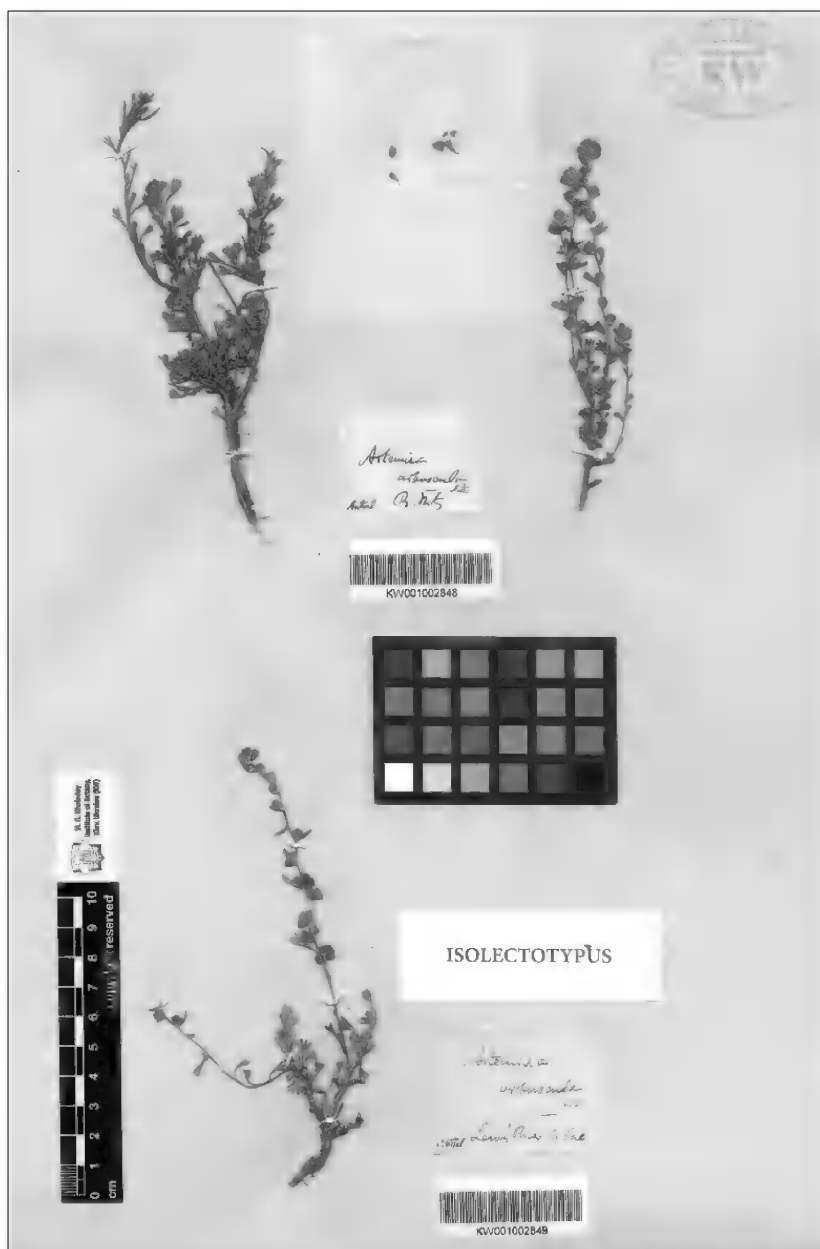
Figure 2. Isolectotype (KW001002849, bottom) and possible isolectotype (KW001002848, top) of *Artemisia arbuscula* Nutt.
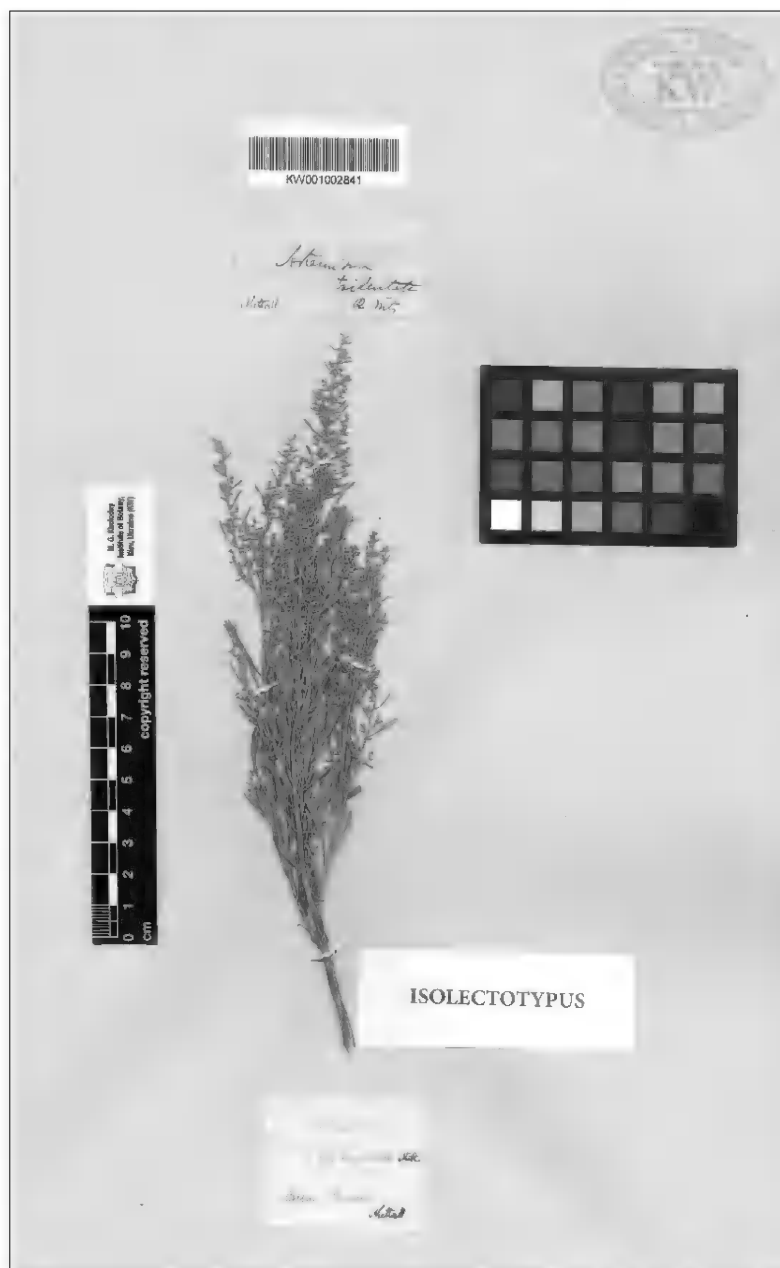
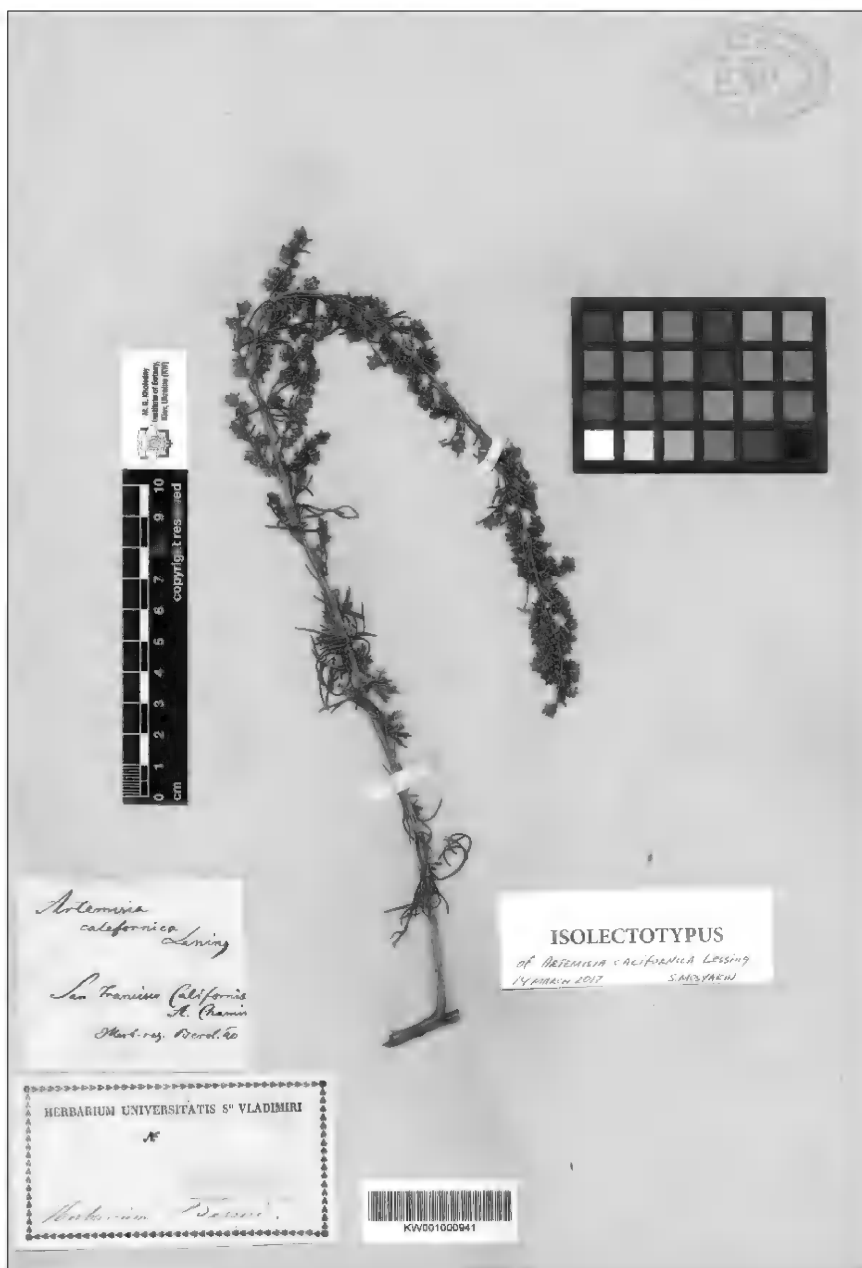Figure 3. Isolectotype of *Artemisia tridentata* Nutt. (KW001002841).

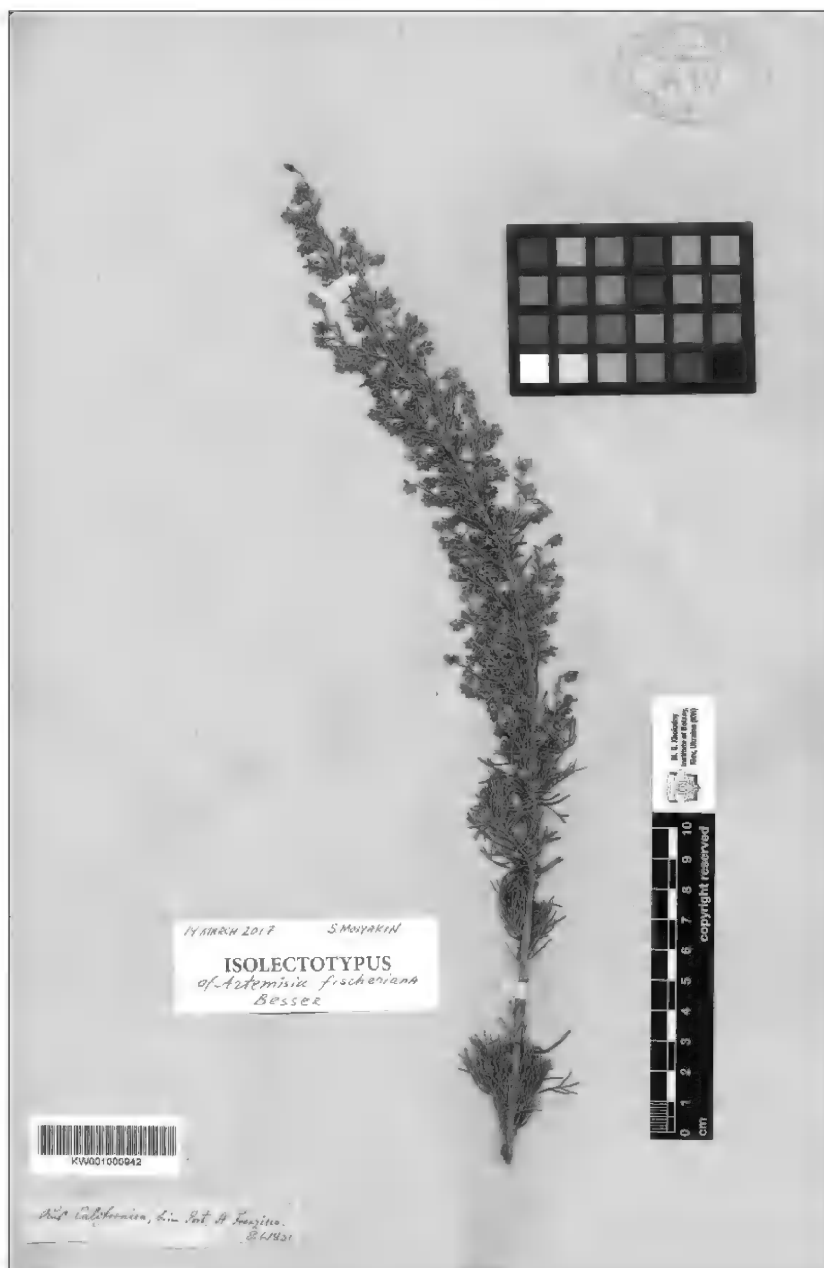Figure 4. Isolectotype of *Artemisia californica* Lessing (KW001000941).

Figure 5. Lectotype of *Artemisia fischeriana* Besser (KW001000943).

Figure 6. Isolectotype of *Artemisia fischeriana* Besser (KW001000942).
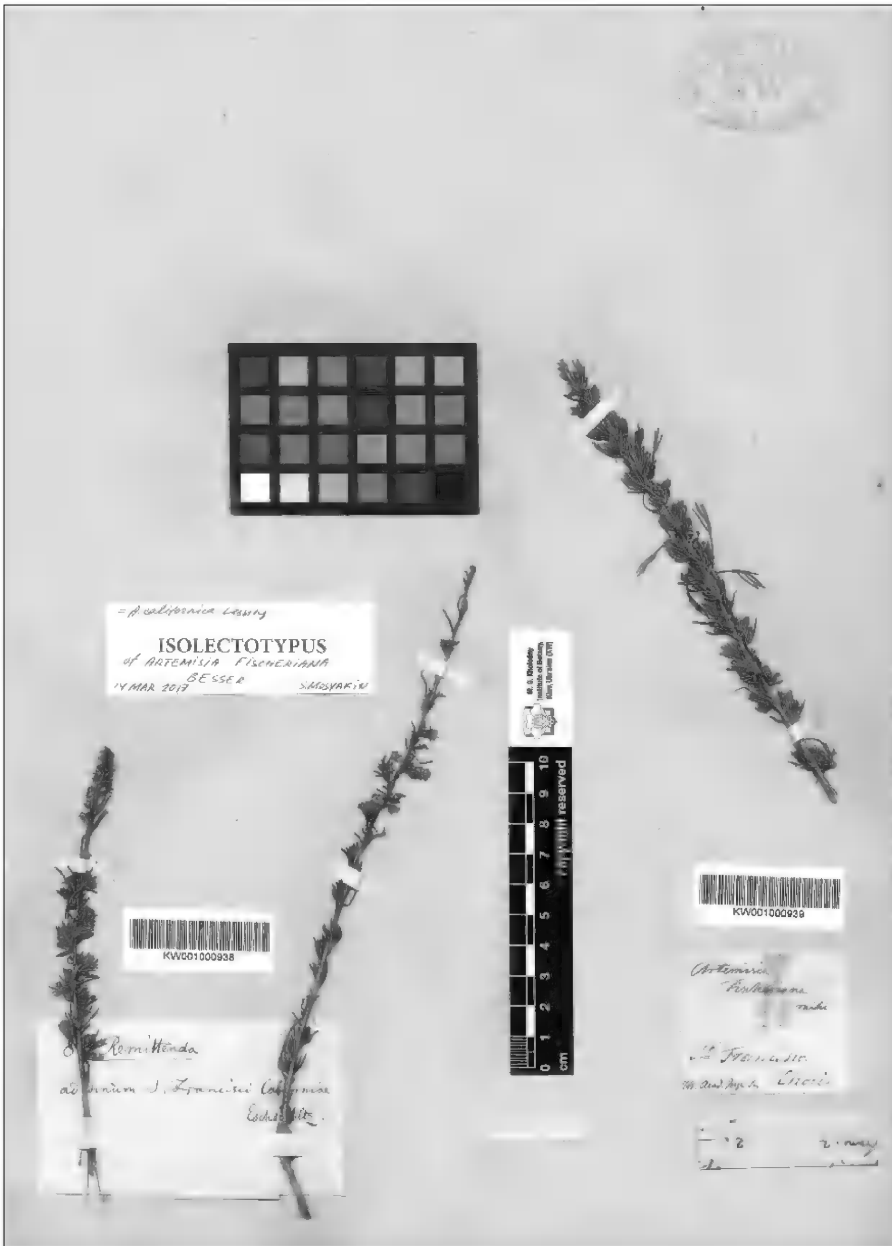
Figure 7. Isolectotype of *Artemisia fischeriana* Besser (KW001000938, left) and a historical specimen collected by L. Choris (KW001000939, right).
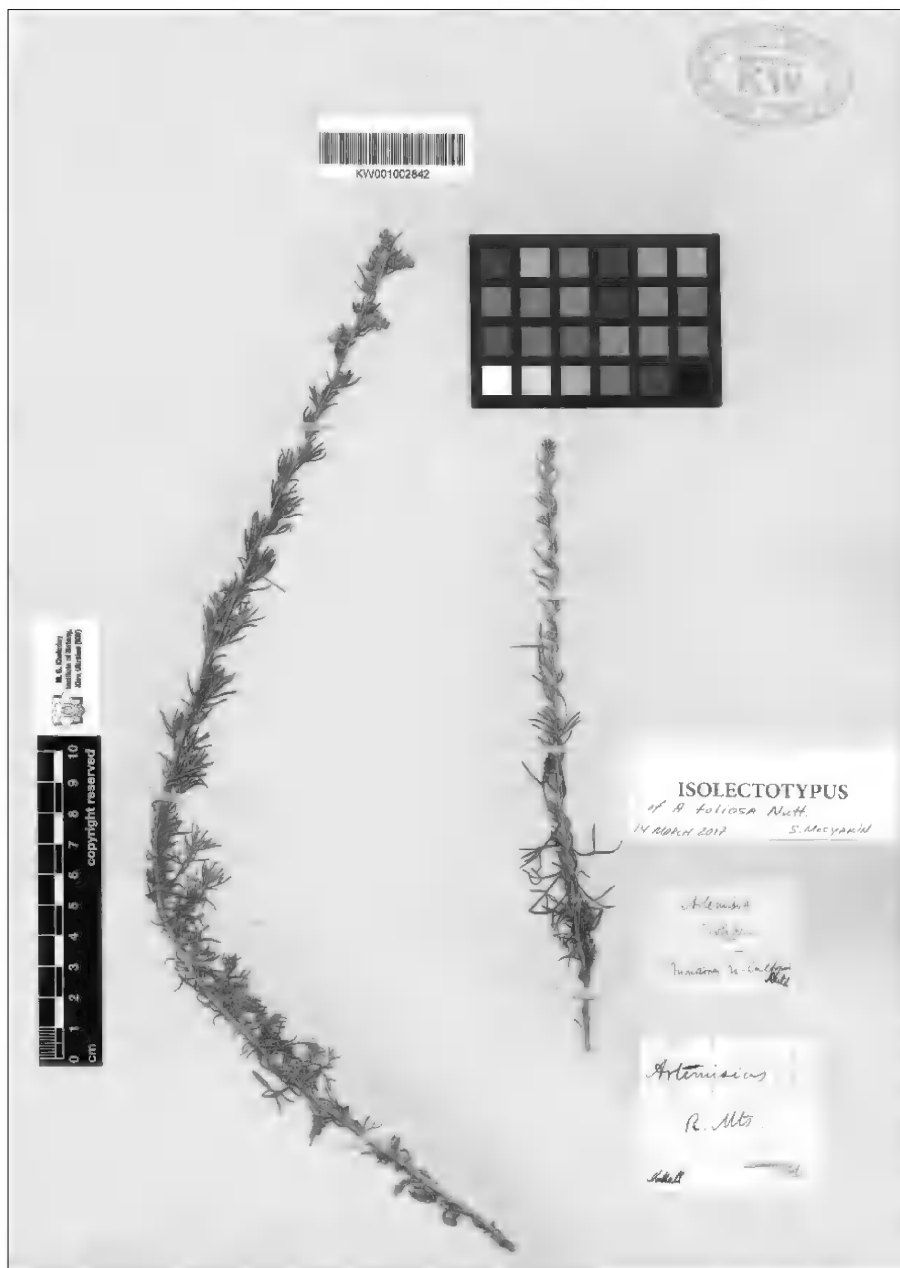
Figure 8. Isolectotype of *Artemisia foliosa* Nutt. (KW001002842).
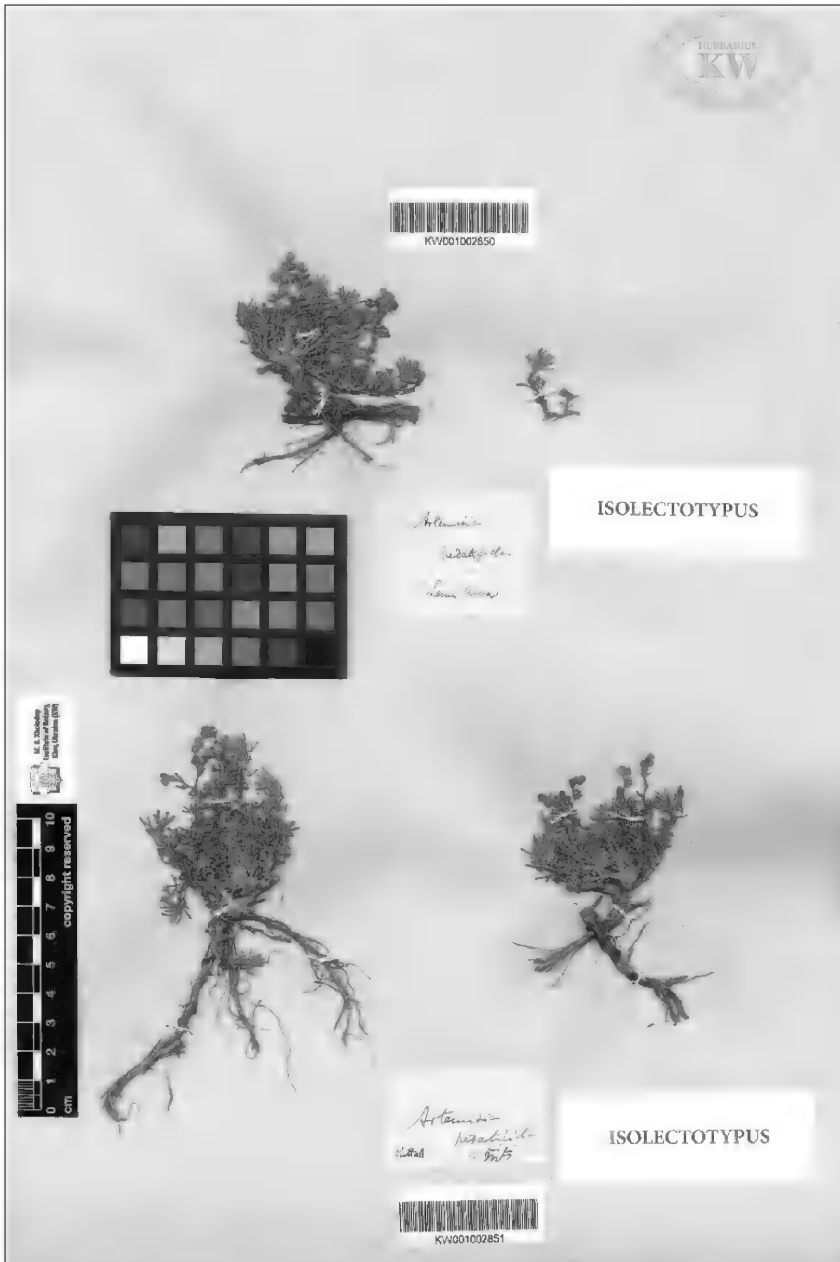
Figure 9. Isolectotypes of *Artemisia pedatifida* Nutt. (KW001002850 and KW001002851).

VASCULAR PLANT SURVEY
OF THE NEOSHO BOTTOMS MANAGEMENT AREA
(GRAND RIVER DAM AUTHORITY)
IN OTTAWA COUNTY, OKLAHOMA

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ABSTRACT
The vascular plant diversity of the Neosho Bottomlands Management Area of the Grand River Dam Authority in northeast Oklahoma, west of Miami (Ottawa County), was documented between October 2014 and November 2016. 937 specimens were obtained from an area of 1021.5 hectares. We documented 460 unique taxa (species, subspecies, varieties) representing 80 families, 254 genera, 450 species, and 10 non-nominal infraspecific taxa. The 78 species and infraspecific taxa exotic to North America represent 16.9% of the total taxa. Twelve species are considered "noxious" by various sources. Five state records were found for Oklahoma, including *Arenaria serpyllifolia* var. *tenuior, Carex sparganioides, Cerastium semidecandrum, Crataegus phaneropyrum,* and *Trifolium aureum* — of these, only the two species of *Carex* are native. In addition to the new state records, 100 taxa were documented for the first time in Ottawa County, 23 of which were non-native. An Annotated Checklist of the taxa is included as an Appendix. Our study increased the number of known unique taxa of vascular plants in Ottawa County by 105 to a total of 1025, representing an increase of 11.4% over its earlier total of 920 species. The large number of state and county level records justifies additional floristic studies in poorly surveyed areas and peripheral regions of states, especially when distant from active herbaria and given that modern distributional data of plants are useful to others besides taxonomists, such as by land use managers.

The Grand River Dam Authority (GRDA) in Oklahoma is a state agency established by the Oklahoma legislature in 1935. Headquartered in Vinita, Oklahoma, it maintains the Grand River waterway in northeast Oklahoma, an area that encompasses all or parts of 24 counties in the state. Its major impoundments include Grand Lake, Lake Hudson, and the Salina Pumped Storage Project.

Among the land holdings of GRDA are numerous, relatively small parcels occurring west of Miami, Ottawa Co., along or near the Neosho River (Figure 1). Ottawa County is the most northeasterly county in Oklahoma and shares its eastern border with McDonald and Newton counties of Missouri and its northern boundary with Cherokee Co., Kansas. The small parcels are known informally as the Neosho Bottoms Management Area (NBMA). They often experience mild to moderate seasonal flooding after high rainfall events that occur mostly in late spring and early summer. Moderate flooding occurred during 2015 and 2016, our two major field seasons, which prevented access to collecting across some areas of the property for up to three weeks. The parcels mostly comprise abandoned or only lightly grazed pastures, active and abandoned pecan groves, and bottomland mixed hardwood forests. A few upland sites somewhat distant from the lower elevations closer to the Neosho River were heavily infested with *Sericea lespedeza* (*Lespedeza cuneata* [see Annotated Checklist for nomenclatural authorities]). As our fieldwork was concluding, some

abandoned pastures were being cleared and burned for grazing via leases (A. Roper, GRDA, pers. comm. 2017), but we did not encounter cleared or burned pastures burned during our fieldwork.

A contractual agreement was signed between GRDA and Pittsburg State University (Pittsburg, Kansas) to inventory the native and non-native vascular plants currently growing on these properties during 2015 and 2016, although some initial collecting occurred in 2014. The purposes of the project were to provide an annotated checklist of vascular plants occurring on the parcels and to provide a reference collection of herbarium specimens for GRDA for its research headquarters in Langley, Oklahoma.

MATERIALS AND METHODS

The study area occurs west of Miami (Figure 1), the county seat of Ottawa County, which has a current population of approximately 13,500 residents based on the 2010 US Census data. The NBMA consists of fourteen parcels of land spread across a north-south axis of ca. 7.4 km (ca. 4.6 miles) and an east-west axis of ca. 4.83 km (ca. 3.0 miles) (Figure 1). All parcels included in this study are located east of South 520 Road. Most also occur west of South 540 Road, with the exception of an outlying parcel bounded on the east by P Street NW (in Miami) somewhat north (but mostly south) of P Street's T-intersection with the east-west oriented West Veteran's Avenue. Apart from one small pasture adjoining it to the north, the parcels occur south of East 65 Road, north of US Hwy 59. All parcels lie north of US Hwy 59/East 110 Road, including the southernmost parcel, which adjoins the highway on its southern boundary. Most of the parcels adjoin one another on at least one border, if one includes those bisected by the Neosho River. A second outlying (non-adjacent) parcel occurs to the southwest of where South 540 Road terminates, ca. 1.0 km due north of a northeast trending bend of the Neosho River. The area we surveyed comprises approximately 1021.5 hectares (ca. 2524 acres).

Our objective in the field was to survey for vascular plants over two complete growing seasons and to obtain at least one specimen of all native, non-native, and naturalizing ornamental plant species occurring in the area. No attempt was made to describe or quantify any aspect of the vegetation ecologically.

Specimens were collected during 2014 (October), 2015 (April through October), and 2016 (April through November), representing 28 separate collecting trips, wherein each trip refers to a single day in the field. Approximately 945 separate specimens were obtained, but a few were discarded due to their sterile condition or if all reproductive material broke off and was lost after pressing and drying. Collecting activities on a given day lasted approximately 2-10 hours, with most being approximately 8 hours. Field trips included from one to three individuals working (mostly) together or occasionally apart. Most collecting was done by the first three authors (see also Acknowledgements). The number of days collected by month included April (4 days), May (5), June (3), July (4), August (6), September (3), October (1), and November (2). On shorter-duration trips, or with specimens that are best preserved if pressed immediately (e.g., specimens of *Sisyrinchium*), pressing sometimes was done the day of the collecting. However, most specimens were kept in plastic bags on ice in coolers overnight and pressed indoors at Pittsburg State University the day after collecting, removed from the physical elements (heat, wind, rain insects) and allowing for more careful pressing and entry or annotation of information in collecting books.

We used the method of "intelligent meandering" to collect the highest possible percentage of plant species growing in the area, wherein collectors walk across parcels through different habitat types at different times during the flowering season to collect at least one of each plant taxon. We did not repeatedly re-collect taxa that were readily identifiable by the naked eye and unlikely to be confused with other species (e.g., the early-blooming and quite distinct species *Phlox divaricata*). However, when in doubt we erred on the conservative side and collected the plant (e.g., species of *Carex*).
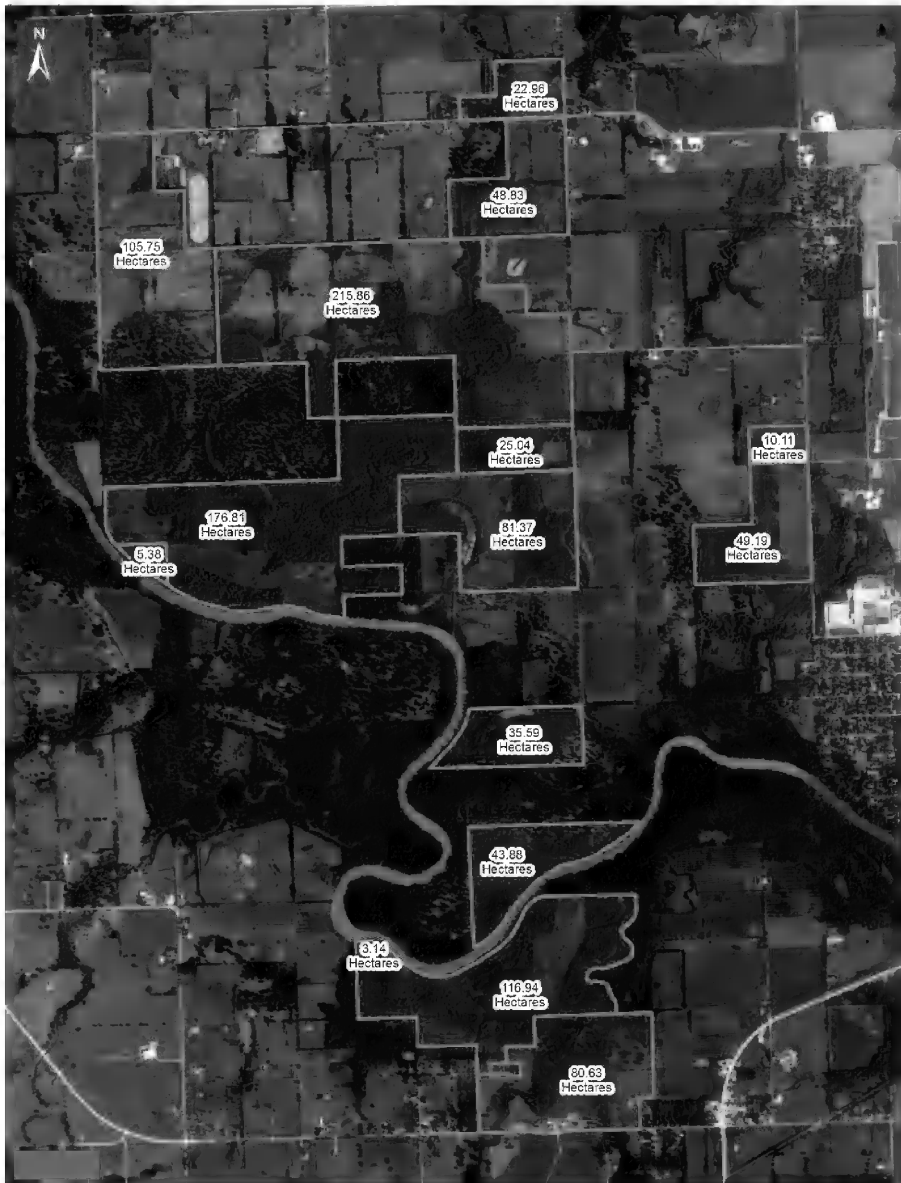
Figure 1.   Parcels (outlined in blue) of the Neosho Bottoms Management Area (Grand River Dam Authority) surveyed for vascular plants, west of Miami, Oklahoma

The first set of herbarium specimens was deposited at the T.M. Sperry Herbarium (KSP, following Thiers 2017) at Pittsburg State University. One duplicate specimen for each taxon (if available) was transferred in a Reference Collection (Snow 2016) to GRDA in Langley, Oklahoma, for future researchers working on projects in the Neosho Bottomlands Management Area. Collection numbers for this project include those Chance Curran (1–353); "Sperry Herbarium Staff" (GRDA 332–542), which were collected by Sam Young but numbered separately from her personal collections; Neil Snow (10787–10813, 10815–10868, 10882–10972); and Karen Stoehr (58–303). Geo-coordinates and elevations were obtained using a hand-held Garmin Montana®, Google Earth maps, or smart phones using WGS84. Specimen data were entered into an Excel spreadsheet following DarwinCore standards (http://rs.tdwg.org/dwc/) and uploaded to Symbiota at Arizona State University (http://Symbiota.org; Gries et al. 2014), the data of which can be accessed from the Consortium of Northern Great Plains Herbaria (http://ngpherbaria.org/portal/index.php). Specimen labels were generated from the Symbiota data portal.

Most identifications relied on Yatskievych (1999, 2006, 2013) as the primary authority, given the proximity of Ottawa County to Missouri, the comprehensive taxonomic details, and relatively recent publication of these three volumes. Secondary sources for identifications or corroboration of identifications from separate sources (especially for the genera *Dichanthelium* and *Carex*), included several volumes of Flora of North America North of Mexico, Flora of The Great Plains (GPFA 1986), Shinners and Mahler's Illustrated Flora of North Central Texas (Diggs et al. 1999), and Flora of Virginia (Weakly et al. 2012).

Although nearly all taxa were identified with a confidence, specific and infraspecific boundaries in *Dichanthelium* continue to be the most difficult and elusive of all North American genera of grasses. Each taxonomic treatment varies substantively in certain ways, and portions of the genus are being actively studied (e.g., Thomas 2015). For this treatment we used primarily the keys in Flora of North America North of Mexico (Freckmann & Lelong 2003) but followed the infraspecific taxa recognized by Kartesz (2017). Given the first author's ontological aversion of recognizing varieties within subspecies (Snow 1997) or, in other words, of accepting taxonomic quadrinomials, for a few genera such as *Symphyotrichum* (Asteraceae), wherein Kartesz (2017) recognizes taxa using both levels, we followed the taxonomy of Yatskievych (2006). In a few instances we included a synonym, as for example when the name reported here is unlikely to occur yet in any regional printed references (e.g., *Buglossoides arvensis* [syn. *Lithospermum arvense*]).

Plant distributions at the state and county levels were based on Kartesz (2017), but we also consulted the Oklahoma Vascular Plants Database of Oklahoma Natural Heritage Inventory (ONHI 2017). Apart from easily confirmed specimens, those representing state records for Oklahoma or records for Ottawa County were compared with authenticated (annotated) specimens in the Missouri-Illinois reference collection at the Missouri Botanical Garden by the first author in November 2016 or the second author in January 2017.

RESULTS

A total of 460 unique taxa of vascular plants (species, subspecies, and varieties) were collected. The taxonomic diversity was spread across 80 families (following APG IV [2016]) and 254 genera, representing 937 separate numbered specimens. Of these, 78 taxa (ca. 16.9%) are not considered native to North America. Our tally of 937 specimens represents an average of approximately 92 collections per square kilometer.

Rank-ordered, the ten most diverse families were Poaceae (67 unique taxa), Asteraceae (52), Cyperaceae (37), Plantaginacae (14), Lamiaceae (13), Polygonaceae (13), Rosaceae (13), Caryophyllaceae (11), Ranunculaceae (11) and Rubiaceae (10). Collectively, these ten families comprised approximately 52.4% of the unique taxa.

The percentages of non-native taxa among these varied significantly, ranging from 2.6% (1 of 39 taxa) in Cyperaceae and 3.9% in Asteraceae, to 44.4% (Fabaceae) and 81.8% (9 of 11 taxa) in Caryophyllaceae. The largest family Poaceae, included 26.4% non-native taxa.

The ten most diverse genera (including ties) comprised 16.9% of the taxa (78 of 460 taxa), including: *Carex* (26 unique taxa [none non-native]), *Juncus* (9 [0]), *Ranunculus* (9 [1]) *Periscaria* (7 [1]), *Dichanthelium* (7 [0]), *Trifolium* (7 [6]), *Croton* (6 [0]), *Plantago* (5 [1]), *Galium* (5 [1]) and *Cerastium* (5 [4]). The percentage of non-native taxa among the ten most diverse genera collectively was only 17.9% (14 of 78 taxa).

None of the Rare or Vulnerable plant species monitored by the US Fish and Wildlife Service were collected (ONHI 2017). Species currently tracked by the Oklahoma Natural Heritage Survey that were collected, including their State and Global ranks (in parentheses), included *Allium triviale* (S2, G5), *Sagittaria ambigua* (S2, G2?), *Iodanthus pinnnatifidus* (S2, G5), *Carex cephalophora* (SNR, G5), *Carex oklahomensis* (S2, G4), *Carya aquatica* (S1, G5), *Forestiera acuminata* (S2, G5), *Dasistoma macrophylla* (S3, G4), *Phanopyrum gymnocarpum* (S1, G5), and *Rumex verticillatus* (S3, G5).

Twelve taxa designated as noxious in Oklahoma by either FOK (2017) or Kartesz (2017) were collected (see Checklist) and are noted for future management considerations of the NBMA. Designations of "noxious" are not always consistent between states, but among those listed by Kartesz (2017) only two are non-native; *Solanum carolinense* var. *carolinense* and *S. elaeagnifolium* are native.

Species of *Rubus* (blackberries) are among the most difficult to identify in North America. Characters typically needed to identify species confidently include growth habit, differentiating between primocanes (first year's growth) and floricanes (flowering, second year's growth), whether canes grow horizontally and root at the nodes, whether canes are mostly straight or arching, and other characters (Widrlechner 2013). Even with authenticated comparative material in the Missouri-Illinois Collection at Missouri Botanical Garden, few specimens could be identified confidently to species level. Specimens of the genus from the 4-state area (KS, OK, MO, AR) are being studied actively by Mark Widrlechner at Iowa State University, who will be returning annotated specimens to local herbaria and which can be used for comparative purposes. We encourage future taxonomists working in the area to adhere closely to recommendations for collecting *Rubus* as outlined by Widrlechner (2013) and also highly recommend capturing digital photos of specimens in the field, which can be attached to herbarium specimens.

DISCUSSION

A total of 920 unique taxa (species, subspecies, and varieties) of vascular plants had been verified for Ottawa Co., Oklahoma, prior to this study (Kartesz 2017). Our results increase that value by 11.4% to a total of 1025 unique taxa, and are notable in three ways. First, they reflect the fact that we have added 5 new state and 100 new records in Ottawa County, but from a sample area within the county of only 1021.5 hectares. Second, over 1 in every 10 specimens collected in the study (11.3 %) represented a first report for the county or state. Third, the results indicate that some counties still are substantially undocumented for their current distribution of vascular plants.

We stress that our data are based primarily on Kartesz (2017), whose research program has been summarizing taxonomic concepts, synonymy, and geographical distributions among North American species of vascular plants for several decades (e.g., Kartesz & Kartesz 1980). These data agree in most cases with those of the Oklahoma Vascular Plant Database records, which were provided to Kartesz and in some cases modified by Kartez (2017). Despite the fact that Ottawa County has the third smallest land area geographically, it is the 14th richest in vascular plant diversity

among the 70 counties in Oklahoma.   Rank-ordered as of March 2017 (Kartesz 2017), they are McCurtain (1675 unique taxa), Bryan (1418), Le Flore (1279), Cleveland (1273), Cherokee (1272), Muskogee (1219), Choctaw (1190), Oklahoma (1180), Murray (1160), Pushmataha (1155), Comanche (1137), Payne (1105), Johnston (1048), and Ottawa (1025).

Disentangling taxonomic concepts and associated nomenclature in the context of geographical distributions can be challenging.   Confounding factors may include changes in taxonomic rank, the merging or segregating of taxa based on newer data, and the use of different taxonomic authorities (often across many decades) during the identification. Although doing so may seem minor today, indicating the authority used for an identification on an annotation label (e.g., "Fl of MO" for *Flora of Missouri*) will aid future workers interpret the basis of our identifications, especially for species-rich or taxonomically difficult genera (e.g., *Carex*, *Dichanthelium*, *Crataegus*). The large number of specimens across numerous institutions in Oklahoma and elsewhere also contributed to the daunting task of trying to confirm every new county record. We thus acknowledge that a few of our first reports may be in error but trust that corrections will be forthcoming as needed.

Parts of northeastern of Ottawa County include localized extensions of the Ozark Plateau limestones, which are shared by areas of northern Arkansas, southern Missouri, and small areas within Cherokee Co., Kansas. Many plant taxa found here have relatively high habitat fidelity to soils derived from these calcareous substrates (Yatskievych 1999). Building upon work dating back to at least the 1950s (Wallis 1959), Hoagland (2007) provided a recent summary of taxa from the Oklahoma Ozarks. Additional results soon after were published from a site east of the Grand River in Ottawa County, which included the limestones (Hoagland & Buthod 2008a). The latter authors also provided of a summary of specimens collected in Ottawa County historically, which then included 2744 specimens. Our tally increases the total for Ottawa County to at least 3681 specimens.

The Neosho Bottoms Management Area does not include extensions of the Ozark Plateau but has moderate levels of plant diversity. The documentation here of so many first-time occurrences in Ottawa County indicates that knowledge of the current distributions of vascular plants in this area of Oklahoma and adjacent areas remains incomplete. This is illustrated further by the fact that the second author (SY), who is completing floristic surveys in nearby Cherokee and Crawford counties, Kansas, has collected numerous records for those two counties and additional state records in the past three years (Young, unpubl.).   Further floristic surveying in other rural and peripheral areas of Oklahoma and other states, especially those that are significantly distant from active herbaria, almost assuredly will yield additional state and county records, similar to results recently documented in rural areas of New York (Martine & Ward 2013).

Although many non-native species occur within Neosho Bottoms Management Area and may predominate in areas such as highly disturbed or abandoned pastures and roadsides, seasonally flooded areas near or adjacent to the Neosho River were seen to harbor mostly native plants. Although future sampling undoubtedly will recover additional taxa, we suspect that our sampling efforts over a period of 36 months have documented at least 90% of the vascular plant taxa currently growing in the Neosho River Management Area.

Prather et al. (2004a, b) documented and discussed the implications of the steady decline in plant collecting across most of North America, compared to rates of collection that had occurred in decades prior to the 1990s. Despite local and relatively recent floristic projects in Oklahoma (e.g., Hoagland & Johnson 2005; Palmer 2007; Hoagland & Buthod 2008b; Channing Richardson & Palmer 2016) and elsewhere in the Great Plains (e.g., Schiebout et al. 2008; Charboneau 2013), the collection density of plant specimens remains inadequate in some areas of the Great Plains and other areas (Taylor 2014). Some areas, such as the NBMA, clearly had not been collected intensively in the past. Despite the concerns raised by Prather et al. (2004a, b), plant collecting in the USA probably

has declined even further, even at a time when knowledge of current plant distributions is highly useful and desirable. For example, the distributional data from our project is providing baseline data that is instrumental for current and future land management decisions for the NBMA (A. Roper, pers. comm. 2016). Given the steady discovery of botanical novelties in North America (e.g., Hartman & Nelson 1998; Ertter 2000; Estes & Small 2007; Legler 2011; Eggers 2013; McDonnell & Fishbein 2016; Crawford & Ayers 2017) and the plethora of newly reported state and county records in our study and elsewhere (e.g., Legler 2010), the importance of targeted floristic work in poorly surveyed areas is easy to justify.

For the more rural parts of Oklahoma, and surely for surrounding states as well, our study suggests that vascular plant diversity at the county level, particularly in and adjacent to wetlands, may be considerably greater than what is currently documented. This was demonstrated previously by the privately published Aquatic Plants of Oklahoma (Nelson & Couch 1985), whose authors surveyed the wetland flora of Oklahoma and added over 240 county records to the state's wetland flora. These records were nearly entirely overlooked for many years. We suspect additional wetland species will be discovered within the NBMA, particularly from areas of shallow standing water or lower-volume feeder streams into the Neosho River, where members of *Potamogeton* and other genera may grow, but which we did not encounter.

Future studies of vascular plants in the NBMA could include classification of the extant vegetation (e.g., USNVC 2016) and more intensive and quantitative surveys of invasive species, with specific recommendations for their management.

ACKNOWLEDGMENTS

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Appendix 1. Annotated checklist of the vascular plants of the Neosho Bottoms Management Area, Grand River Dam Authority, Ottawa County, Oklahoma.

The Checklist is organized by spore-bearing plants (Ferns and Fern-Allies), Gymnosperms, and Angiosperms. All taxa are arranged alphabetically beginning with plant family. Vernacular or common names are provided (primarily following Kartesz 2017). Common names for infraspecific taxa are not provided. The wetland status of the US Fish and Wildlife Services (see Lichvar 2013) follows the common name, as such information may prove useful to future workers, including employees of GRDA who manage the site. "Unranked" refers to taxa that currently lack USFWS wetland rankings, but these are usually upland taxa. Taxa non-native to North America are indicated as "Non-native" in bold. State and county records also are noted in bold, with commentary (generally) on the taxon's distribution in Oklahoma, locally near Ottawa County, and frequently regionally. The "4-State area" refers to counties occurring nearby in Kansas (to the north), Missouri (to the east), and Arkansas (to the east and south).

FERNS AND FERN-ALLIES

Aspleniaceae (Spleenwort family)
Asplenium platyneuron (L.) B.S.P. Ebony spleenwort. FACU-, FACU

Ophioglossaceae (Adder's-tongue family)
Sceptridium dissectum (Spreng.) Lyon. Cut-leaf grape-fern. FAC. **Ottawa County record.** Reported
    from eight counties previously in Oklahoma and adjacent counties to the north (KS) and east
    (MO). Voucher: *C. Curran 285 & S. Young*

Woodsiaceae (Cliff-fern family)
Woodsia obtusa (Spreng.) Torr. subsp. *obtusa*. Blunt-lobe cliff fern. Unranked

GYMNOSPERMS

Cupressaceae (Cyperus family)
Juniperus virginiana L. var. *virginiana*. Eastern red-cedar. FACU-, FACU

ANGIOSPERMS

Acanthaceae (Acanthus family)
Dicliptera brachiata (Pursh) Spreng. Branched foldwing. FACW
Ruellia humilis Nutt. Finger-leaf wild petunia. UPL, FAC-
Ruellia strepens L. Limestone wild petunia. FAC-, FAC

Aceraceae (Maple family)
Acer negundo L. var. *negundo*. Ash-leaf maple (or Boxelder). FAC*, FACW
Acer saccharinum L. Silver maple. FAC, FACW

Adoxaceae (Muskroot family)
Sambucus nigra (L.) subsp. c*anadensis* (L.) R. Bolli. Black elderberry. UPL, FACW
Viburnum prunifolium L. Smooth blackhaw. FACU, FAC-

Agavaceae (Agave family)
Camassia scillioides (Raf.) Cory. Atlantic camas. FAC, FACW

Alismataceae (Water-plantain family)
Alisma triviale Pursh. Northern water-plantain. Unranked (but likely OBL). **Ottawa County record.**
    Reported from Alfalfa and Grant counties in northcentral OK; known in adjacent Newton and
    McDonald counties (MO). Voucher: *Sperry Herbarium Staff 430.*
Sagittaria ambigua J. G. Sm. Kansas arrowhead. OBL

Alliaceae (Onion family)
Allium canadense L. var. *canadense*. Meadow garlic. FACU-, FACU. **Noxious.**
Allium canadense L. var. *lavendulare* (Bates) Ownbey & Aase. **Noxious. Ottawa County record.**
    Reported from fourteen counties in OK and all counties adjacent except for Craig Co, OK.
    Voucher: *C. Curran 20 & N. Snow*
Allium canadense L. var. *mobilense* (Regel) Ownbey. **Noxious.**
Allium tricoccum Ait. var. *tricoccum*. Ramp. FACU, FACU+. **Noxious. Ottawa County record.**
    Reported from OK thus far only from LeFlore county in the southeast; the other nearest reported
    occurrence is from Carter County in southeast MO. Voucher: *K. Stoehr 191 & S. Young*
Allium vineale L. subsp. *compactum* (Thuill.) Coss. & Germ. Crow garlic. FACU, FACU-. **Noxious.
    Non-native**
Nothoscorum bivalve (L.) Britt. Crowpoison. FACU-, FAC

Amaranthaceae (Amaranth family)
Amaranthus palmeri S. Wats. Careless weed. FACU-, FACU
Amaranthus spinosus L. Spiny amaranth. FACU-, FACU
Amaranthus tuberculatus (Moq.) Sauer. Rough-fruit amaranth. FACU-, OBL
Chenopodium album L. var. *missouriense* (Aellen) I.J. Bassett & C.W. Crompton. UPL, FAC
Dysphania ambrosioides (L.) Mosyakin & Clemants. Mexican tea. **Non-native**. UPL, FAC.
Iresene rhizomatosa Standl. Juda's-bush. FACW-, FACW. **Ottawa County record.** Reported from
    many counties in eastern OK and known from all adjacent counties except Craig County (OK).
    Voucher: *C. Curran 288 & S. Young*

Anacardiaceae (Sumac family)
Rhus copallinum L. Winged sumac. UPL*, FACU
Toxicodendron radicans (L.) Kuntze subsp. *radicans*. Eastern poison ivy. FACU, FACW

Apiaceae (Parsely or Carrot family)
Chaerophyllum tainturieri Hook. Hairy-fruit chervil. UPL, FACW
Limnosciadium pinnatum (DC.) Mathias & Constance. Tansy dogshade. FAC-+, OBL. **Ottawa
    County record.** Reported for over 25 counties in eastern OK and known from adjacent counties
    to the north, west and east. Vouchers: *C. Curran 129 & S. Young*; *Sperry Herbarium Staff 419*.
Ptilimnium nuttallii (DC.) Britt. Laceflower. FAC+, FACW+
Sanicula canadensis L. var. *canadensis*. Canadian black-snakeroot. UPL*, FACU+
Sanicula odorata (Raf.) K.M. Pryer & L.R. Phillippe. Clustered black-snakeroot. FACU, FAC+
Torilis arvensis (Huds.) Link subsp. *arvensis.* Spreading hedge-parsely. Unranked. **Non-native**
Zizia aurea (L.) W.D.J. Koch. Meadow alexanders. UPL, FAC-

Apocynaceae (Dogbane family)
Amsonia tabernaemontana Walt. var. *tabernaemontana*. Eastern bluestar. FACW-, FACW
Apocynum androsaemifolium L. Spreading dogbane. UPL
Asclepias incarnata subsp. *incarnata* L. Swamp milkweed. FACW+, OBL
Asclepias longifolia Michx. var. *hirtella* (Pennell) B.L. Turner. UPL, FAC
Asclepias viridis Raf. Green comet milkweed. Unranked
Gonolobus suberosus (L.) R. Br. var. *granulatus* (Scheele) Krings & Q.Y. Yang. Angular-fruited
    anglepod. FACW*, FACW

Aquifoliaceae (Holly family)
Ilex decidua Walt. Deciduous holly. FACW-, FACW

Araceae (Arum family)
Arisaema dracontium (L.) Schott. var. *dracontium*. Greendragon. FACW
Lemna minor L. Common duckweed. OBL. **Ottawa County record.** Reported from less than half of
    the counties in OK but widespread; known from most counties adjacent to or near Ottawa County.
    Voucher: *N. Snow 10941 & S. Young*

Asteraceae (Aster family)
Achillea millefolium L. Common yarrow. UPL, FACU
Ageratina altissima (L.) King & Robins. var. *altissima*. White snakeroot. UPL, FACU
Ambrosia artemisiifolia L. Annual ragweed. UPL, FACU+
Ambrosia bidentata Michx. Lance-leaf ragweed. Unranked
Ambrosia trifida L. Giant ragweed. FACU-, FACW
Bidens aristosa (Michx.) Britt. Bearded beggarticks. FACW
Bidens bipinnata L. Spanish needles. Unranked

Bidens frondosa L. Devil's pitchfork. FACW, FACW+. **Ottawa County record.** Widespread across much of the USA and has been reported for all adjacent counties (Kartesz 2017). Vouchers: *C. Curran et al. 276.*

Boltonia asteroides (L.) L'Hér. var. *latisquama* (Gray) Cronq. White doll's daisy. Unranked

Bradburia pilosa (Nutt.) Semple. Soft bradbury-bush. Unranked

Cirsium altissimum (L.) Spreng. Tall thistle. Unranked

Coreopsis tinctoria Nutt. var. *tinctoria*. Golden tickseed. FACU, FAC

Echinacea pallida (Nutt.) Nutt. var. *pallida*. Pale purple-coneflower. Unranked

Eclipta prostrata (L.) L. False daisy. FAC, OBL

Elephantopus carolinianus Raeusch. Carolina elephant's-foot. FACU, FAC

Erigeron annuus (L.) Pers. Eastern daisy fleabane. FACU*, FAC

Erigeron canadensis L. Canadian horseweed. UPL, FAC. **Non-native**

Erigeron strigosus Muhl. ex Willd. var. *strigosus*. FACU, FAC

Erigeron tenuis Torr. & Gray. Slender-leaf fleabane. Unranked

Eupatorium serotinum Michx. Late-flowering thoroughwort. FAC-, FAC+

Euthamnia gymnospermoides Greene. Texas goldentop. FAC, FACW

Gamochaeta argyrinea Nesom. Silvery everlasting. Unranked

Helenium amarum (Raf.) H. Rock var. *amarum*. Yellowdicks. FACU-, FACU

Helenium flexuosum Raf. Purple-head sneezeweed. FAC-, FACW

Helianthus grosseserratus Martens. Sawtooth sunflower. FAC*, FACW

Helianthus mollis Lam. Ashy sunflower. Unranked

Iva annua L. Annual marsh-elder. FAC*, FAC

Krigia caespitosa (Raf.) Chambers var. *caespitosa*. Weedy dwarf-dandelion. FACU, FAC

Krigia dandelion (L.) Nutt. Potato dwarf dandelion. FACU*, FAC

Lactuca canadensis L. Canadian blue lettuce. FACU-, FAC+

Packera glabella (Poir.) C. Jeffrey. Cross-leaf groundsel. FACW, OBL

Packera obovata (Muhl. ex Willd.) W.A. Weber & A. Löve. Round-leaf groundsel. FACU-*, FACU-

Pyrrhopappus carolinianus (Walt.) DC. Carolina desert-chicory. Unranked

Rudbeckia hirta L. var. *hirta*. Black-eyed Susan. FACU-, FACU

Rudbeckia laciniata L. var. *laciniata*. Green-head coneflower. FACU, FACW+

Rudbeckia triloba L. var. *triloba*. Brown-eyed Susan. FACU-, FAC-

Senecio hieraciifolius L. var. *hieraciifolius*. American burnweed. FACU, FAC

Silphium perfoliatum L. var. *perfoliatum*. Cup-plant. FACU, FACW

Solidago altissima L. subsp. *altissima*. Tall goldenrod. UPL, FACU+

Solidago altissima L. subsp. *gilvocanescens*. Tall goldenrod. Not ranked.

Solidago gigantea Ait. Late goldenrod. FAC*, FACW

Solidago missouriensis Nutt. Missouri goldenrod. Unranked

Symphyotrichum ericoides (L.) Nesom var. *ericoides*. White heath American-aster. UPL, FACU

Symphyotrichum lanceolatum (Willd.) Nesom var. *lanceolatum*. White-panicled American-aster. FAC*, FACW. **Ottawa County record.** This taxon is widespread and occurs in all adjacent counties (Kartesz 2017). Vouchers: *N. Snow et al. 10805; N. Snow et al. 10916; C. Curran et al. 280.*

Symphyotrichum pilosum (Willd.) Nesom var. *pilosum*. White oldfield American-aster. UPL, FAC-

Symphyotrichum praealtum (Poir) Nesom var. *praealtum*. Willow-leaf American-aster. FACW-, OBL

Taraxacum officinale G.H. Weber ex Wiggers. Common dandelion. UPL, FACW **Non-native**

Verbesina alternifolia (L.) Britt. ex Kearney. Wingstem. FAC, FACW

Verbesina virginica L. White crownbeard. UPL, FACU

Vernonia arkansana DC. Arkansas ironweed. FAC*, FACW

Vernonia baldwinii Torr. Western ironweed. UPL, FACW-

Xanthium strumarium L. Rough cockleburr. FACU, FAC+

Betulaceae (Birch family)
Betula nigra L. River birch. FACW, OBL

Bignoniaceae (Trumpet-creeper family)
Campsis radicans (L.) Seem. ex Bureau. Trumpet-creeper. FACU*, FAC

Boraginaceae (Borage family)
Buglossoides arvensis (L.) I.M. Johnst. Corn-gromwell. Unranked. **Non-native** [synonym:
    Lithospermum arvense L.]
Heliotropium indicum L. Indian heliotrope. FAC, FACW

Brassicaceae (Mustard family)
Capsella bursa-pastoris (L.) Medik. Shephard's purse. UPL, FAC
Cardamine hirsuta L. Hairy bittercress. UPL, FAC. **Non-native. Ottawa County record.** Known
    from about half the counties in eastern Oklahoma and virtually all in Arkansas and Louisiana; in
    Missouri mostly known from the southern and eastern halves of the state. Vouchers: *N. Snow
    10829 & K. Stoehr; C. Curran 58 & S. Young*
Cardamine parviflora L. Sand bittercress. FACU, FACW
Draba brachycarpa Nutt. ex Torr. & Gray. Short-pod whitlow-grass. Unranked
Iodanthus pinnatifidus (Michx.) Steud. Purple-rocket. FACW-, OBL
Lepidium campestre (L.) Ait. f. Cream-anther field pepperwort. Unranked. **Non-native. Ottawa
    County record.** Widespread across Missouri, northwest Arkansas, eastern Kansas, and with
    fewer reports from southern and eastern Oklahoma. Voucher: *K. Stoehr 300 & S. Young.*
Lepidium densiflorum Schrad. Miner's peppwort. UPL, FAC
Lepidium virginicum L. var. *virginicum.* Poor-man's pepperwort. UPL*, FAC-
Rorippa palustrus (L.) Bess. subsp. *palustris.* Bog yellowcress. FAC, OBL
Rorippa sessiliflora (Nutt.) A.S. Hitchc. Stalkless yellowcress. FACW+, OBL

Campanulaceae (Bellflower family)
Lobelia cardinalis L. Cardinal-flower. FACW+, OBL
Lobelia inflata L. Indian-tobacco. FACU-, FAC. **Ottawa County record.**
Triodanis perfoliata (L.) Nieuwl. subsp. *biflora* (Ruíz & Pavón) Lammers. Clasping-leaf Venus'
    looking-glass. Unranked
Triodanis perfoliata (L.) Nieuwl. subsp. *perfoliata.* UPL, FAC

Cannabaceae (Hemp family)
Celtis laevigata Willd. Sugar-berry. UPL, FACW
Celtis occidentalis L. Common hackberry. FACU, FAC

Caprifoliaceae (Honeysuckle family)
Lonicera japonica Thunb. Japanese honeysuckle. UPL, FACU+. **Non-native**
Lonicera sempervirens L. Trumpet honeysuckle. FACU, FAC
Symphoricarpos orbiculatus Moench. Coralberry. UPL, FAC-

Caryophyllaceae (Pink family)
Arenaria serpyllifolia L. var. *serpyllifolia.* Thyme-leaf sandwort. UPL, FAC. **Non-native**
Arenaria serpyllifolia L. var. *tenuior* Mert. & Koch. Thyme-leaf sandwort. Unranked. **Non-native.
    Oklahoma State record.** Known from over twenty counties in northern Arkansas, including
    adjacent McDonald County and many others in Missouri. Material is limited but the seed with of
    ca. 0.4 mm agrees with the key in Yatskievych (2006: 798). Voucher: *K. Stoehr 244 & S. Young*
Cerastium brachypetalum Desportes ex Pers. Gray mouse-ear chickweed. Unranked. **Non-native**

Cerastium brachypodum (Englem. ex Gray) B.L. Robins. Short-stalk mouse-ear chickweed. FACU-, FAC. **Ottawa County record.** Reported from over half of the counties in OK and known from most adjacent counties in the 4-state area. Voucher: *K. Stoehr 87 et al.*

Cerastium fontanum Baumg. subsp. *vulgare* (Hartman) Greuter & Burdet. FACU-, FAC-. **Non-native. Ottawa County record.** Reported for approximately half the counties in eastern OK and known from adjacent counties to the north, east and south. Voucher. *N. Snow 10817 & K. Stoehr.*

Cerastium glomeratum Thuill. Sticky mouse-ear chickweed. UPL*, FACU **Non-native**

Cerastium semidecandrum L. Five-stamen mouse-ear chickweed. Unranked. **Non-native. Oklahoma State record.** Reported sporadically from Texas (Hopkins County), LA (five parishes), and a few counties each in MO and AR. Vouchers: *K. Stoehr 150 et al.*; *K. Stoehr 233 & S. Young*

Dianthus armeria L. Deptford pink. UPL, FACU-. **Non-native**

Silene stellata (L.) Ait. f. Widow's frill. Unranked

Stellaria media (L.) Vill. Common chickweed. UPL*, FACU **Non-native**

Stellaria neglecta Weihe. Greater chickweed. Unranked. **Non-native. Ottawa County record.** As currently reported this species is considered largely absent from the 4-state area. However, extensive recent floristic research in Cherokee and Crawford counties in KS (S. Young, ined.) indicates the species is quite common. Vouchers: *K. Stoehr 60 et al.*; *K. Stoerh 65 et al.*; *K. Stoehr 79 et al.*

Celastraceae (Bittersweet family)

Elaeodendron fortunei Turcz. Winter-creeper. Unranked. **Non-native. Ottawa County record.** Known in adjacent Cherokee County (KS) and McDonald County (MO); otherwise only known from Muskogee and Pittsburg counties in Oklahoma. Voucher: *C. Curran 350 et al.*

Commelinaceae (Spiderwort family)

Commelina diffusa Burm. f. var. *diffusa*. Climbing dayflower. FAC, FACW. **Ottawa County record.** Reported from fourteen counties in eastern OK; known from Cherokee County (KS) to the north and Newton County (MO) to the east. Voucher: *N. Snow 10947 & S. Young*

Commelina erecta L. White-mouth dayflower. FAC

Tradescantia bracteata Small. Long-bract spiderwort. UPL, FAC

Trandescantia ohiensis Raf. Bluejacket. FACU, FACW

Convolvulaceae (Morning -glory family)

Cuscuta cuspidata Englem. Cusp dodder. Unranked (parasitic vine)

Cuscuta cephalanthi Engelm. Buttonbrush dodder. Unranked (parasitic vine). **Ottawa County record.** Reported from Oklahoma (county not verified; Kartesz 2017) and known from adjacent McDonald County, MO. Voucher. *N. Snow 10939 & S. Young*

Cuscuta gronovii Willd. ex J.A. Schultes var. *gronovii*. Scaldweed. Unranked (parasitic vine). **Ottawa County record.** Reported in OK from over 25 counties, including Delaware County due south; also known from adjacent counties to the east and north. Vouchers: *C. Curran 217 & S. Young*; *N. Snow 10804 et al.*

Ipomoea hederacea Jacq. Ivy-leaf morning-glory. FACU*, FAC

Ipomoea lacunosa L. Whitestar. FAC+, FACW

Ipomoea pandurata (L.) G.F.W. Mey. Man-of-the-earth. FACU-, FAC-

Ipomoea purpurea (L.) Roth. Common morning-glory. UPL, FAC. **Noxious. Non-native.**

Cornaceae (Dogwood family)

Cornus drummondii C.A. Mey. Rough-leaf dogwood. FAC

Cyperaceae (Sedge family)

Carex annectens (Bickn.) Bickn. Yellow-fruit sedge. FAC+, FACW+

Carex arkansana (Bailey) Bailey. Arkansas sedge. Unranked. **Ottawa County record.** Known in only seven widely-spaced counties in eastern OK, the nearest being Osage and Wagoner counties; reported in adjacent Cherokee County (KS). Vouchers: *C. Curran 35 & N. Snow, K. Stoehr 227 & S. Young, K. Stoehr 181 & S. Young, K. Stoehr 182 & S. Young*

Carex blanda Dewey. Eastern woodland sedge. FACU*, FAC

Carex brevior (Dewey) Mackenzie. Short-beak sedge. UPL, OBL

Carex bushii Mackenzie. Bush's sedge. FAC, OBL

Carex caroliniana Schwein. Carolina sedge. FACU, OBL. **Ottawa County record.** Known in central and eastern Oklahoma from approximately eighteen counties, the nearest being Cherokee County; known from adjacent Cherokee (KS) and Newton (MO) counties. At the time of re-submission the OK Vascular Plants Database is inconsistent, showing Ottawa County as being represented, but with the one voucher listed identified as *Carex bushii*. Voucher: *K. Stoehr 238 & S. Young*

Carex cephalophora Muhl. ex Willd. Oval-leaf sedge. UPL*, OBL

Carex conjuncta Boott. Soft fox sedge. FAC, FACW. **Ottawa County record.** Reported from Nowata and Rogers counties (OK); known from adjacent McDonald and Newton counties (MO) and Cherokee County (KS). Voucher: *K. Stoehr 171 & S. Young*

Carex crus-corvi Shuttlw. ex Kunze. Raven-foot sedge. OBL. **Ottawa County record.** Known form over two dozen counties in eastern OK and from adjacent Cherokee County, KS.

Carex davisii Schwien. & Torr. Davis' sedge. FACU, FAC+. **Ottawa County record.** Known from eight counties in eastern OK (including Delaware County to the due south) and adjacent counties in KS and MO. Vouchers: *C. Curran 47 & S. Young; K. Stoehr 124 et al.; K. Stoehr & 173 & S. Young; K. Stoher 174 & S. Young*

Carex festucacea Schukr. ex Willd. Fescue sedge. FAC, FACW. **Ottawa County record.** Recorded for twenty counties across much of OK. Voucher: *K. Stoehr 197 & S. Young*

Carex frankii Kunth. Frank's sedge. OBL

Carex grisea Wahlen. Inflated narrow-leaf sedge. Unranked. **Ottawa County record.** Widespread in central and eastern OK; known from adjacent counties in KS, MO and OK. Vouchers: *K. Store* [and collectors] *101*; 103; 116; 118; 168; 170; 237; 239; *N. Snow 10969 & C. Curran; N. Snow 10832 & K. Stoehr.*

Carex grayi Carey. Gray's sedge. FACW, FACW+

Carex hyalinolepis Steud. Shoreline sedge. OBL.

Carex leavenworthii Dewey. Leavenworth's sedge. Unranked

Carex lupuliformis Sartwell ex Dewey. False hop sedge. FACW+, OBL

Carex molesta Mackenzie ex Bright. Troublesome sedge. FACU, FACW. **Ottawa County record.** Reported thus far from only six counties in OK, but including adjacent Delaware Co., and known from adjacent counties in KS and MO. Voucher: *Sperry Herbarium Staff 344.*

Carex molestiformis Reznicek & P. Rothr. Ozark Plateau sedge. Unranked. **Ottawa County record.** Reported from at least six counties in eastern OK, including adjacent Delaware County, and known from about twenty counties eastwards in northern and central AR. Vouchers: *K. Stoehr 225 & S. Young.*

Carex muhlenbergii Schkuhr ex. Willd. var. *enervis* Boott. Muhlenberg's sedge. Unranked

Carex oklahomensis Mackenzie. Oklahoma sedge. FACW, OBL

Carex radiata (Wahlenb.) Small. Eastern star sedge. Unranked.

Carex rosea Schkuhr ex. Willd. Rose's sedge. Unranked. **Ottawa County record.** Known in OK from Bryan, McCurtain and Le Flore counties; reported from adjacent Cherokee (KS) and McDonald and Newton (MO) counties. Vouchers: *C. Curran 65 & S. Young;* K*. Stoehr 246 & S. Young*

Carex shortiana Dewey. Short's sedge. FAC, FACW+

Carex socialis Mohlenbrock & Schwegm. Low woodland sedge. Unranked. **Ottawa County record.** Reported from Oklahoma previously six counties in the southeastern and eastern part of the state and Cleveland County, the nearest being Delaware County; known elsewhere east and south in

the lower Mississippi and Ohio river drainages (including AR and MO) and the Blackland Prairies and Cross Timbers and Prairies of Texas (regions following Gould [1962]) and sporadically east to the Carolinas and Georgia (Kartesz 2017; Weakly et al. 2012). The senior collectors' notes indicate "rare" at this locality, which was a seasonally flooded mixed deciduous forest. Voucher: *N. Snow 10856 et al.*

Carex sparganioides Muhl. ex Willd. Burr-reed sedge. FACU, FAC+. **Oklahoma State record.** Reported from adjacent Newton and McDonald counties (MO) and nearby Crawford and Labette counties (KS); evidently not common in Arkansas or Kansas (Kartesz 2017) but north and east through the upper Midwest and New England. Details of the population size were not noted, so we are unable report on its relative abundance. The two collections cited were collected at the same site; the second collection cited here was taken because of uncertainty whether it was the same taxon as the other collection. Vouchers: *K. Stoehr 123 et al., K. Stoehr 129 et al.*

Cyperus acuminatus Torr. & Hook. ex Torr. Taper-tip flat sedge. OBL

Cyperus echinatus (L.) Wood. Globe flat sedge. FACU, FAC+

Cyperus erythrorhizos Muhl. Red-root flat sedge. FACW+, OBL

Cyperus iria L. Ricefield flat sedge. FACW, FACW+. **Non-native. Ottawa County record.** Known from five counties in eastern OK, the nearest being Osage County; mostly occurring farther east and south. Vouchers: *Sperry Herbarium Staff 522.*

Cyperus pseudovegetus Steud. Marsh flat sedge. FACW

Cyperus squarrosus L. Awned flat sedge. FACW+, OBL

Cyperus strigosus L. Straw-color flat sedge. FACW, FACW+

Eleocharis acicularis (L.) Roemer & J.A. Schultes. Needle spike-rush. OBL

Eleocharis engelmannii Steud. Engelmann's spike rush. FACW, OBL. **Ottawa County record.** Widespread in central and eastern Oklahoma and known from adjacent counties in KS, MO and OK. Voucher: *N. Snow 10920 & S. Young; Sperry Herbarium Staff 432.*

Eleocharis obtusa (Willd.) J.A. Schultes. Blunt spike rush. OBL.

Isolepis carinata Hook. & Arn. ex Torr. Keeled lateral-bulrush. FACW, OBL

Ebenaceae (Ebony family)
Diospyros virginiana L. Common persimmon. FACU, FAC

Euphorbiaceae (Spurge family)
Acalypha monococca (Engelm. ex Gray) L. Mill. & Gandhi. Single-seed three-seed mercury. Unranked

Acalypha rhomboidea Raf. Common three-seed mercury. FACU-, FAC-. **Ottawa County record.** Known from many counties in OK (apart from the panhandle), including adjacent Delaware County; also in adjacent portions of AR, KS and MO. Vouchers: *C. Curran 239 & S. Young; C. Curran 279 & S. Young*

Croton glandulosus L. var. *septentrionalis* Muell.-Arg. Vente-conmigo. Unranked

Croton lindheimeri (Engelm. & Gray) Engelm. & Gray ex Wood. Lindheimer's croton. Unranked. **Ottawa County record**. Reported from fourteen counties in southern and eastern OK (Kartesz 2017), the nearest being Muskogee County; collections from AR, KS, and MO far less frequent and none within ca. 200 km. Voucher: *N. Snow 10882 & S. Young*

Euphorbia dentata var. dentata Michx. Toothed spurge. Unranked

Euphorbia maculata L. Spotted sandmat. UPL, FACU-

Euphorbia nutans Lag. Eyebean. FACU-, FAC

Euphorbia spathulata Lam. Warty spurge. FACU-, FAC. **Ottawa County record.** Known from over half the counties in OK and KS and many in AR and MO, including adjacent counties in OK, KS, and MO. Voucher: *C. Curran 78 & S. Young*

Fabaceae (Pea family)

Amorpha fruticosa L. False indigo-bush. FAC*, OBL

Amphicarpaea bracteata (L.) Fern. American hog-peanut. FACU, FACW

Baptisia alba (L.) Vent. var. *macrophylla* (Larisey) Isely. FACU*, FAC

Cercis canadensis L. var. *canadensis*. Redbud. UPL, FAC

Chamaecrista nictitans (L.) Moench subsp. *nictitans*. Partridge-pea. UPL, FACU

Desmanthus illinoiensis (Michx.) MacM. ex B.L. Robins. & Fern. Prairie bundle-flower. UPL, FAC

Desmodium glabellum (Michx.) DC. Dillenius' tick-trefoil. Unranked. **Ottawa County record.**
    Known from OK in several counties in eastern OK including adjacent Delaware County; common
    in southern MO but much less so in AR and KS. Voucher: *C. Curran 254 & S. Young*

Desmodium paniculatum (L.) DC. Panicled-leaf tick-trefoil. UPL, FAC-

Desmodium perplexum Schub. Perplexed tick-trefoil. Unranked

Gleditsia triacanthos L. Honeylocust. FACU, FAC

Kummerowia stipulacea (Maxim.) Makino. Korean-clover. UPL, FACU-. **Non-native**

Lathyrus pusillus Ell. Tiny vetchling. UPL*, FACW-. **Ottawa County record.** In OK known from
    approximately 25 counties, the nearest being Rogers County; reported as extirpated from MO but
    once known from adjacent Newton County, and rare in five southeast counties of KS, including
    adjacent Cherokee County. Voucher: *K. Stoehr 96 et al.*

Lespedeza cuneata (Dum.-Cours.) G. Don. Chinese bush-clover. UPL*, FAC. **Non-native**

Medicago lupulina L. Black medik. UPL, FAC. **Non-native**

Melilotus officinalis (L.) Lam. Yellow sweet-clover. UPL, FACU-. **Non-native**

Mimosa nuttallii (DC.) B.L. Turner. Nuttall's mimosa. Unranked.

Senna marilandica (L.) Link. Maryland wild sensitive-plant. FAC, FACW

Sesbania herbacea (P. Mill.) McVaugh. Peatree. FAC, FACW. **Ottawa County record.** Reported for
    many counties in eastern OK, the nearest being Mayes and Nowata counties; widespread in much
    of AR (where it is a noxious weed) but much less so in KS and MO but not in adjacent counties.
    Voucher: *C. Curran 185 & S. Young*

Strophostyles helvola (L.) Ell. Trailing fuzzy-bean. FACU-, FAC+

Trifolium arvense L. Rabbit-foot clover. Unranked. **Non-native. Ottawa County record.** Common in
    adjacent parts of OK, AR and MO but not southeast KS. Voucher: *Sperry Herbarium Staff 386.*

Trifolium aureum Pollich. Greater hop clove. Unranked. **Non-native. Oklahoma State record.** This
    species is widely distributed in North America, with concentrations in the USA in the northern
    Rockies, the upper Midwest (MN, WI, MI), the northeast, and along the Appalachian ridges. The
    nearest reports are from Dade and Christian counties in Missouri, approximately 100 and 150 km
    northwest and east, respectively. Voucher: *C. Curran 49 & S. Young*

Trifolium campestre Schreb. Lesser hop clover. Unranked

Trifolium dubium Sibthorp. Suckling clover. UPL, FACU. **Non-native. Ottawa County record.**
    Common in adjacent parts of OK, AR, KS and MO. Voucher: *N. Snow 10790 et al.*

Trifolium hybridum L. Alsike clover. UPL, FAC. **Non-native.**

Trifolium pratense L. Red clover. UPL, FAC. **Non-native**

Trifolium repens L. White clover. FACU-, FAC. **Non-native**

Vicia sativa L. Garden vetch. UPL, FACW. **Non-native. Ottawa County record.** Reported from
    approximately twenty counties in OK, the nearest being Mayes Co., and adjacent Newton and
    McDonald counties in Missouri. Voucher: *K. Stoehr 119 et al.*

Vicia villosa Roth subsp. *varia* (Host) Corb. Winter vetch. **Non-native. Ottawa County record.**
    Known from over half the counties in eastern OK, the nearest being Cherokee and Nowata
    counties; occurring in adjacent counties in KS and MO. Voucher: *C. Curran 40 & S. Young*

Fagaceae (Oak family)

Quercus macrocarpa Michx. var. *macrocarpa*. Burr oak. FACU, FAC

Quercus palustris Muenchh. Pin oak. FAC, FACW

Quercus rubra L. Northern red oak. FACU-, FACU+
Quercus shumardii Buckl. Shumard's oak. FAC, FACW-

Gentianaceae (Gentian family)
Sabatia angularis (L.) Pursh. Rose-pink. FAC, FAC+. **Ottawa County record.** Known from the
adjacent counties of Delaware (OK), Cherokee (KS), and McDonald and Newton (both MO); also
reported from over half of the counties of eastern Oklahoma. Vouchers: *C. Curran 117 & S.
Young*; *Sperry Herbarium Staff 354.*

Geraniaceae (Geranium family)
Geranium carolinianum L. Carolina crane's-bill. Unranked
Geranium dissectum L. Cut-leaf crane's-bill. Unranked. **Non-native. Ottawa County record.**
Scattered widely across seven counties in OK, the nearest being Pittsburg, Co.; know from nearby
Labette County (KS) and Washington County (AR). Vouchers: *N. Snow 10836 et al.*; *K. Stoehr
195 & S. Young*; *C. Curran 91 & S. Young*

Haloragacae (Water-milfoil family)
Myriophyllum heterophyllum Michx. Two-leaf water milfoil. OBL. **Ottawa County record.** Reported
in OK from fifteen counties, the nearest being Mayes County; known in adjacent Newton (MO)
and Cherokee County (KS) and many counties in adjacent states of AR, KS, and MO. Vouchers:
C. Curran 44 & S. Young; *Sperry Herbarium Staff 371 & 372*

Hemerocallidaceae (Day-lily family)
Hemerocallis fulva (L.) L. Orange day-lily. UPL, FACU. **Non-native. Ottawa County record.**
Known in OK from Le Flore and Cherokee counties; reported in many nearby counties in AR,
KS, and MO. Voucher: *Sperry Herbarium Staff 438*

Hypericaceae (St. John's Wort family)
Hypericum perforatum L. Common St. John's-wort. Unranked. **Non-native**

Iridaceae (Iris family)
Sisyrinchium angustifolium P. Mill. Narrow-leaf blue-eyed grass. FACU, FACW-

Juglandaceae (Walnut family)
Carya aquatica (Michx. f.) Nutt. Water hickory. OBL. **Ottawa County record.** Known from
Oklahoma infrequently in seven southeastern counties and Cherokee County of east-central OK
(Kartesz 2017). Although the specimen was sterile and only starting to exhibit peeling bark, the
number of leaflets and the densely pubescent abaxial midvein together confirm its identification.
Carya cordiformis (Wangenh.) K. Koch. Bitter-nut hickory. FACU+, FAC
Carya illinoinensis (Wangenh.) K. Koch. Pecan. FACU, FACW
Carya ovata (P. Mill.) K. Koch. Shag-bark hickory. FACU, FACU+
Carya tomentosa (Lam. ex Poir.) Nutt. Mockernut hickory. Unranked

Juncaceae (Rush family)
Juncus brachycarpus Engelm. White-root rush. FACW. **Ottawa County record.** Widespread in OK
and adjacent states of AR, KS, and MO, and known from all adjacent counties. Voucher: *Sperry
Herbarium Staff 378.*
Juncus vel aff. *debilis* Gray. Weak rush. FACW*, OBL. If correctly identified, it would be a county
record. (This record is not included in the numerical tallies.) Voucher: *Stoehr 211 & S. Young.*
Noted as infrequent at this locality.
Juncus diffusissimus Buckl. Slim-pod rush. FACW, FACW+

Juncus effusus L. subsp. *solutus* (Fern. & Weig.) Hänet-Ahti. Lamp rush. FACW, OBL
Juncus interior Wieg. var. *interior*. Interior rush. FACU, FACW
Juncus marginatus Rostk. Bog rush. FACW, OBL
Juncus scirpoides Lam. Needle-pod rush. FACW, FACW+
Juncus secundus Beauv. ex Poir. Lopsided rush. FACU, FAC. **Ottawa County record.** Reported from
    twelve counties in OK, the nearest being Adair and Nowata counties; present in adjacent
    McDonald County (MO) and occurring in much of AR and MO. Voucher: *C. Curran 141 & S.
    Young*
Juncus tenuis Willd. Lesser poverty-rush. FAC-, OBL
Juncus torreyi Coville. Torrey's ruish. FACW, FACW+

Lamiaceae (Mint family)
Hedeoma hispida Pursh. Rough false pennyroyal. Unranked
Lamium purpureum L. Giraffe-head. **Non-native.** Unranked
Lycopus americanus Muhl. ex W. Bart. Cut-leaf water-horehound. OBL
Lycopus rubellus Moench. Taper-leaf water-horehound. OBL
Monarda fistulosa L. var. *fistulosa*. Oswego-tea. UPL, FAC+ [species-level rank]
Monarda fistulosa L. var. *mollis* (L.) Benth. UPL, FAC+ [species-level rank]
Perilla frutescens (L.) Britt. var. *frutescens*. Beef-steak plant. FACU+, FAC+. **Non-native**
Physostegia virginiana (L.) Benth. subsp. *praemorsa* (Shinners) Cantino. Obedient-plant. FACW
Prunella vulgaris L. subsp. *lanceolata* (W. Bart.) Hultén. Common selfheal. FACU, FACW [species-
    level rank]
Pycnanthemum tenuifolium Schrad. Narrow-leaf mountain-mint. FACU, FACW
Scutellaria parvula Michx. Small skullcap. UPL, FACU
Stachys tenuifolia Willd. Smooth hedge-nettle. FAC, OBL
Teucrium canadense L. var. *occidentale* (Gray) McClintock & Epling. FAC+, FACW [species-level
    rank]. **Ottawa County record.** Reported from ten counties in OK, the nearest being Cherokee
    County; scattered occurrences across much of KS and MO, but none within ca. 150 km. Voucher:
    Sperry Herbarium Staff 337.

Lauraceae (Laurel family)
Lindera benzoin (L.) Blume. Northern spicebush. FACW-, FACW

Lythraceae (Loosestrife family)
Ammannia coccinea Rottb. Valley redstem. OBL
Lythrum alatum Pursh var. *alatum*. Wing-angle loosestrife. FACW+, OBL
Lythrum alatum Pursh var. *lanceolatum* (Ell.) Torr. & Gray ex Rothrock. Wing-angle loosestrife.
    FACW+, OBL [species-level rank]. **Ottawa County record.** Widespread in OK and AR, not
    reported for KS and known from only two counties in eastern and central MO. Vouchers: *C.
    Curran 123*; *C. Curran 182 & S. Young*
Rotala ramosior (L.) Koehne. Lowland toothcup. OBL

Malvaceae (Mallow family)
Abutilon theophrasti Medik. Velvetleaf. UPL, FACU-. **Non-native**
Hibiscus laevis All. Halberd-leaf rose-mallow. OBL
Hibiscus trionum L. Flower-of-an-hour. Unranked. **Non-native**
Sida spinosa L. Prickly fanpetals. UPL*, FACU

Menispermaceae (Moonseed family)
Cocculus carolinus (L.) DC. Carolina coralbead. FACU, FAC
Menispermum canadense L. Canadian moonseed. FACU*, FAC

Molluginaceae (Carpetweed family)
Mollugo verticillata L. Green carpetweed. FAC-, FAC

Montiaceae (Candy-flower family)
Claytonia virginica L. var. *virginica*. Virginia spring-beauty. FACU-, FAC

Moraceae (Mulberry family)
Maclura pomifera (Raf.) Schneid. Osage-orange. UPL, FACU
Morus alba L. White mulberry. UPL, FAC. **Non-native**
Morus rubra L. Red mulberry. FACU, FAC

Nyctaginacaeae (Four-O'clock family)
Mirabilis nyctaginea (Michx.) MacM. Heart-leaf four-o'clock. UPL*, FACU. **Ottawa County record.** Widespread across 4-state area including all adjacent counties, apart from Craig County (OK). Voucher: *C. Curran 64 & S. Young*

Oleaceae (Olive family)
Forestiera acuminata (Michx.) Poir. Eastern swamp-privet. OBL
Fraxinus pennsylvanica Marsh. Green ash. FAC, FACW
Ligustrum sinense Lour. Chinese privet. UPL*, FAC. **Non-native**
Ligustrum vulgare L. European privet. UPL, FAC-*. **Non-native. Ottawa County record.** Reported from ten counties in OK, the nearest being Tulsa County; not reported for adjacent counties in AR, KS, or MO, but of these states most common in AR. Voucher: *K. Stoehr 303 & S. Young*

Onagraceae (Evening primrose family)
Ludwigia palustris (L.) Ell. Marsh primrose-willow. OBL
Ludwigia peploides (Kunze) Raven subsp. *glabrescens* (Kunze) Raven. OBL. **Ottawa County record.** Common regionally for at least 300 km in all directions; known from adjacent counties in AR, MO, and KS. Voucher: *N. Snow 10955 & S. Young*
Oenothera filiformis (Small) W.L. Wagner & Hoch. Long-flower evening-primrose. Unranked
Oenothera laciniata Hill. Cut-leaf evening-primrose. UPL, FAC*
Oenothera villosa Thunb. subsp. *villosa*. Hairy evening-primrose. FACU, FACW*

Orchidaceae (Orchid family)
Spiranthes vernalis Engelm. & Gray. Spring ladies'-tresses. FAC, FACW

Orobanchaceae (family)
Agalinis heterophylla (Nutt.) Small ex Britt. Prairie false foxglove. FACU+, FAC+
Dasistoma macrophylla (Nutt.) Raf. Mullein-foxglove. FACU-, FAC. **Ottawa County record.** Reported from eighteen counties in OK, including adjacent Delaware and Craig counties; also occurring in most adjacent and nearby counties in AR, KS and MO. Voucher: *C. Curran 274 & S. Young*

Oxalidaceae (Wood-sorrel family)
Oxalis dillenii Jacq. Yellow wood-sorrel. FACU*. **Ottawa County record.** Known from many counties across most of OK (excluding the Panhandle and approximately twenty contiguous counties in east-central parts of the state; in adjacent Delaware County and widespread and common across most of AR, KS, and MO. Vouchers: *K. Stoehr 185 & S. Young*; *K. Stoehr 288 & S. Young*; *C. Curran 34 & N. Snow*; *C. Curran 48 & S. Young*; *N. Snow 10841 et al.*

Passifloraceae (Passion-flower family)
Passiflora incarnata L. Purple passion-flower. Unranked
Passiflora lutea L. Yellow passion-flower. Unranked

Penthoraceae (Ditch-Stonecrop family)
Penthorum sedoides L. Ditch-stonecrop. OBL

Phrymaceae (Lopseed family)
Mimulus alatus Ait. Sharp-wing monkey-flower. OBL

Phytolaccaceae (Pokeweed family)
Phytolacca americana L. var. a*mericana*. American pokeweed. FACU*, FAC

Plantaginaceae (Plantain family)
Bacopa rotundifolia (Michx.) Wettst. Disk water-hyssop. OBL
Callitriche heterophylla Pursh subsp. *heterophylla*. Greater water-starwort. OBL
Gratiola neglecta Torr. Clammy hedge-hyssop. OBL
Nuttallanthus canadensis (L.) D.A. Sutton. Oldfield-toadflax. Unranked
Nuttallanthus texanus (Scheele) D.A. Sutton. Texas-toadflax. Unranked
Penstemon tubiflorus Nutt. var. *tubiflorus*. White-wand beardtongue. Unranked
Plantago aristata Michx. Large-bract plantain. Unranked
Plantago elongata Pursh. Prairie plantain. UPL, FACW+
Plantago lanceolata L. English plantain. UPL, FACW **Noxious. Non-native**
Plantago rugelii Dcne. Black-seed plantain. FACU, FAC
Plantago virginica L. Plain-seed plantain. UPL, FACW
Veronica arvensis L. Corn speedwell. UPL, FAC. **Non-native**
Veronica peregrina L. subsp. *peregrina*. Neckweed. FACU-, OBL
Veronica peregrina L. subsp. *xalapensis* (Kunth) Pennell. Neckweed. Unranked

Platanaceae (Planetree family)
Platanus occidentalis L. American sycamore. FAC, FACW

Poaceae (Grass family)
Agrostis hyemalis (Walt.) B.S.P. Winter bent. FACU, FACW
Agrostis perennans (Walt.) Tuckerman. Upland bent. FACU, FACW. **Ottawa County record.**
    Reported for ten counties in OK, including adjacent Delaware County; known from adjacent
    Newton (MO) and Cherokee (KS) counties, and widespread in AR and MO. Voucher: *Sperry
    Herbarium Staff 367.*
Alopecurus carolinianus Walt. Tufted meadow-foxtail. FAC+, FACW **Ottawa County record.**
    Known in OK from over half the counties across all but the Panhandle of OK, including adjacent
    Delaware County; widespread in nearby AR, KS and MO. Voucher: *K. Stoehr 89 et al.*
Andropogon gerardi Vitman. Big bluestem. FACU, FAC
Aristida oligantha Michx. Prairie three-awn. Unranked
Bothriochloa laguroides (DC.) Hunter subsp. *torreyana* (Steud.) Allred & Gould. Silver beardgrass.
    Unranked
Bromus arvensis L. Field brome. UPL, FACU. **Non-native**
Bromus catharticus Vah. var. *catharticus*. Rescue grass. Unranked. **Non-native. Ottawa County
    record**. Widespread across OK, southern KS, and AR; known from adjacent Newton County
    (MO). Vouchers: *K. Stoehr 241 & S. Young, K. Stoehr 284 & S. Young; C. Curran 37 & N.
    Snow.*
Bromus racemosus L. Bald brome. Unranked. **Non-native**

Bromus tectorum L. Cheat grass. Unranked. **Non-native**

Chasmanthium latifolium (Michx.) Yates. Indian wood-oats. UPL, FACW

Chloris verticillata Nutt. Tumble windmill-grass. Unranked. **Ottawa County record.** Widespread across OK, KS, southwestern MO and a few counties in AR; occurs in adjacent Newton and McDonald counties (MO). Voucher: *N. Snow 10894 & S. Young*

Cinna arundinacea L. Sweet wood-reed. FACW, OBL*

Coleataenia anceps (Michx.) Soreng. Beaked cut-throat grass. FAC-, FACW

Coleataenia rigidula (Bosc ex Nees) LeBlond subsp. *rigidula*. Red cut-throat grass. FAC, OBL

Cynodon dactylon (L.) Pers. Bermuda grass. FACU, FAC. **Non-native**

Dactylis glomerata L. subsp. *glomerata*. Orchard grass. UPL, FACU+. **Ottawa County record.** Widespread in AR, KS and MO, and sixteen counties in OK, including adjacent Delaware County. Voucher: *K. Stoehr 283 & S. Young*

Diarrhena obovata (Gleason) Brandenburg. Hairy beakgrain. Unranked

Dichanthelium aciculare (Desv. ex Poir.) Gould & C.A. Clark. Needle-leaf rosette grass. FACU-, FACU. **Ottawa County record.** Known from eight counties in OK; reported most closely from Benton County, AR. Voucher: *C. Curran 51 & S. Young*

Dichanthelium acuminatum (Sw.) Gould & C.A. Clark var. *acuminatum*. Tapered rosette grass. FACU-, FACW

Dichantelium commutatum (J.A. Schultes) Gould. Variable rosette grass. FACU+, FAC. **Ottawa County record.** Reported from eight counties in eastern OK and known from adjacent Delaware County (OK) and McDonald County (MO); widespread farther east and south. Voucher: *K. Stoehr 202 & S. Young*

Dichanthelium latifolium (L.) Harville. Broad-leaf rosette grass. FACU-, FACU. **Ottawa County record.** Known from adjacent McDonald and Newton counties in MO and Cherokee County, KS. Voucher: *C. Curran 44 & S. Young*

Dichanthelium malacophyllum (Nash) Gould. Soft-leaf rosette grass. Unranked. **Ottawa County record.** Known from only four counties in OK, the nearest being Sequoyah and Creek counties; widespread in MO and in adjacent in Newton and McDonald (MO) and Cherokee (KS) counties. Voucher: *C. Curran 53 & S. Young*

Dichanthelium scoparium (Lam.) Gould. Broom rosette grass. FAC, FACW. **Ottawa County record.** Known from over half the counties of eastern OK; reported for all adjacent counties except McDonald County, MO. Voucher: *Sperry Herbarium Staff 393*.

Dichanthelium sphaerocarpon (Ell.) Gould var. *isophyllum* (Scribn.) Gould & C.A. Clark. Round-seed rosette grass. FACU. **Ottawa County record.** Known from eighteen counties in eastern OK, including adjacent Delaware and Craig coungties; also in adjacent Cherokee (KS) and McDonald (MO) counties. Vouchers: *K. Stoehr 201 & S. Young, K. Stoehr 204 & S. Young*

Digitaria ciliaris (Retz.) Koel. Southern crab grass. FAC. **Non-native**

Digitaria cognata (J.A. Schultes) Pilger. Carolina crab grass. Unranked

Digitaria filiformis (L.) Koel. var. *filiformis*. Slender crab grass. Unranked. **Ottawa County record.** Known from at least ten other counties in eastern and southern OK; reported for adjacent counties in Missouri and Cherokee County (KS). Voucher: *N. Snow 10914 & S. Young*

Digitaria ischaemum (Schreb. ex Schweib.) Schreb. ex Muhl. Smooth crab grass. UPL, FAC*. **Non-native.**

Digitaria sanguinalis (L.) Scop. Hairy crab grass. UPL, FAC-. **Non-native**

Dinebra panicea (Retz.) P.M. Peterson & N. Snow subsp. *mucronata* (Michx.) P.M. Peterson & N. Snow. FACW

Echinochloa crus-galli (L.) Beauv. Large barnyard grass. FACU, OBL. **Non-native**

Echinochloa muricata (Beauv.) Fern. var. *muricata*. Rough barnyard grass. FAC, OBL

Eleusine indica (L.) Gaertn. Indian goose grass. UPL, FAC. **Non-native**

Elymus glabriflorus (Vasey) Scribn & Beal. Southeastern wild rye. Unranked. **Ottawa County record.** Widespread in the 4-state area; known from all adjacent counties except for Craig County

(OK). Voucher: *C. Curran 110 & S. Young*; *Sperry Herbarium Staff 343*; *Sperry Herbarium Staff 404.*

Elymus virginicus L. var. *virginicus.* Virginia wild rye. FAC, FACW

Eragrostis hirsuta (Michx.) Nees. Big-top love grass. UPL, FACU

Eragrostis pectinacea (Michx.) Nees var. *pectinacea.* Purple love grass. FACU, FAC. **Ottawa County record.** Reported for adjacent counties apart from Craig County (OK), and widespread and common in the region. Voucher: *C. Curran 224 & S. Young*

Festuca subverticillata (Pers.) Alexeev. Nodding fescue. FACU, FAC

Hordeum pusillum (Ledeb.) J.A. Schultes. Prairie koeler's grass. Unranked (but clearly an upland species)

Leersia lenticularis Michx. Catchfly grass. OBL. **Ottawa County record.** Known from adjacent Cherokee County (KS) to the north, four other counties in eastern OK, and fairly widespread in the Mississippi and lower Ohio River drainages. Voucher: *C. Curran 255 & S. Young*

Leersia oryzoides (L.) Sw. Rice cut grass. OBL.

Lolium perenne L. var. *multiflorum* (Lam.) Husnot. Perennial ryegrass. UPL. **Non-native. Ottawa County record.** Known from adjacent counties; widespread regionally and in eastern OK. Vouchers: *K. Stoehr 189-A & S. Young*; *C. Curran-70 & S. Young*

Muhlenbergia bushii Pohl. Nodding muhly. Unranked

Muhlenbergia schreberi J.F. Gmel. Nimblewill. FACU*, FACU

Panicum dichotomiflorum Michx. var. *dichotomiflorum.* Fall panic grass.

Paspalum laeve Michx. Field crown grass. FAC, FACW-. **Ottawa County record.** Widespread in eastern OK and regionally. Vouchers: *N. Snow 10899 & S. Young*; *N. Snow 10962 & S. Young*; *Sperry Herbarium Staff 422.*

Paspalum pubiflorum Rupr. ex Fourn. Hairy-seed crown grass. FAC, FACW

Paspalum setaceum Michx. Slender crown grass. UPL*, FAC

Phanopyrum gymnocarpum (Ell.) Nash. Savannah panic-grass. OBL. **Ottawa County record.** Reported as rare in McCurtain, Cleveland and Cherokee counties (OK); known from the southern third of AR and mostly south and east. Voucher: *C. Curran 183 & S. Young*

Phleum pratense L. Timothy. Common timothy. FACU*, FAC. **Non-native. Ottawa County record.** Sporadically reported (four counties) from central and eastern OK but probably more common; widespread reports in adjacent KS, MO, and AR. Vouchers: *K. Stoehr 166 & S. Young*; *K. Stoehr 222 & S. Young*; *C. Curran 28 & N. Snow*; *C. Curran 125.*

Poa annua L. Annual bluegrass. FACU-, OBL. **Non-native.**

Poa compressa L. Flat-stem bluegrass. FACU-, FAC. **Non-native. Ottawa County record.** Reported from several counties across much of OK; widespread elsewhere, especially northward. Voucher: *K. Stoehr 126 & S. Young*

Poa pratensis L. subsp. *pratensis.* Kentucky bluegrass. FACU-, FACU. **Ottawa County record.** This subspecies is widespread in much of OK and North America. That it is first reported here reflects the fact that many common species are under-collected. Vouchers: *N. Snow 10831 & K. Stoehr*; *C. Curran 22 & N. Snow*; *K. Stoehr 213 & S. Young*

Schedonorus arundinaceus (Schreb.) Dumort. Tall false rye grass. UPL, FACW-. **Non-native. Ottawa County record.** Widespread across North America and with many reports in Oklahoma. Vouchers: *K. Stoerh 149 & S. Young*; *K. Stoehr 272 & S Young*; *Sperry Herbarium Staff 432*; *C. Curran 33 & N. Snow.*

Schedonorus pratensis (Huds.) Beauv. Meadow false rye grass. FACU-, FAC. **Non-native. Ottawa County record.** Widespread across North America and with many reports in Oklahoma. Voucher: *K. Stoehr 274 & S. Young*

Schizachyrium scoparium (Michx.) Nash var. *scoparium.* Little false bluestem. UPL, FAC+

Setaria parviflora (Poir.) Kerguélen. Marsh bristle grass. FACU

Setaria viridis (L.) Beauv. *var. viridis.* Green bristle grass. **Non-native.** Unranked

Sorghum halepense (L.) Pers. Johnson grass. **Noxious. Non-native.** FACU-, FAC

Spartina pectinata Bosc ex Link. Freshwater cord grass. FACW, OBL

Sporobolus airoides (Torr.) Torr. Alkali-sacaton. FAC-, FAC. **Ottawa County record.** Reported for over twenty counties in (mostly) western OK, the nearest being Cherokee County; unknown from adjacent counties in AR, KS, and MO. Voucher: *N. Snow 10963 & S. Young*

Steinchisma hians (Ell.) Nash. Gaping grass. FACW-, OBL. **Ottawa County record.** Reported for most counties in eastern OK and AR. However, this is the most northerly occurrence in Oklahoma. Voucher: *Sperry Herbarium Staff 381.*

Tridens flavus (L.) A.S. Hitchc. var. *flavus.* Tall redtop. UPL, FACU

Tridens strictus (Nutt.) Nash. Long-spike fluff grass. FACU, FACW

Tripsacum dactyloides (L.) L. Eastern mock grama. FAC, FACW

Vulpia octoflora (Walt.) Rydb. var. *octoflora.* UPL, FACU+

Polemoniaceae (Phlox family)

Phlox divaricata L. Wild blue phlox. UPL, FACU

Polygonaceae (Buckwheat family)

Persicaria amphibia (L.) S.F. Gray p.p. Water smartweed. OBL. **Ottawa County record.** Widespread in OK and elsewhere in North America. Vouchers: *N. Snow 10809 et al.*; *C. Curran 199 & S. Young; C. Curran 232 & S. Young*

Persicaria bicornis (Raf.) Nieuwl. Pink knotweed. Unranked

Persicaria hydropiper (L.) Delarbre. Mid water-pepper. FACW*, OBL. **Non-native**

Persicaria hydropiperoides (Michx.) Small. Swamp smartweed. OBL

Persicaria lapathifolia (L.) S.F. Gray. Dock-leaf smartweed. FAC, OBL

Persicaria punctata (Ell.) Sm. Spotted smartweed. FACW, OBL

Persicaria virginiana (L.) Gaertn. Jumpseed. FAC, FACW

Polygonum aviculare L. subsp. *depressum* (Meisn.) Arcang. FACU*, FAC. **Non-native**

Polygonum ramosissimum Michx. subsp. *ramosissimum.* Yellow-flower knotweed. FACU-, FACW. **Ottawa County record.** Widespread across much of OK, including adjacent Delaware County, and regionally, although less common in AR. *C. Curran 188 & S. Young*

Rumex acetosella L. Common sheep sorrel. UPL, FACW. **Noxious. Non-native**

Rumex altissimus Wood. Pale dock. FACW, FACW+

Rumex crispus subsp. *crispus.* Curly dock. FAC. **Non-native**

Rumex verticillatus L. Swamp dock. FACW*, OBL. **Non-native. Ottawa County record.** Known infrequently in OK from several counties in the central and eastern parts of the state; more commonly east in MO and AR, where it is listed as a noxious weed. The closest report is from Cherokee County (KS) to the north. Vouchers: *C. Curran 12 & N. Snow; Sperry Herbarium Staff 338.*

Portulacaceae (Pursland family)

Portulaca oleracea L. Little hogweed. FACU, FAC

Primulaceae (Primrose family)

Androsace occidentalis Pursh. Western rock-jasmine. FACU-, FACU

Lysimachia ciliata L. Fringed yellow-loosestrife. FACW-, FACW+

Lysimachia nummularia L. Creeping-jenny. FACW-, OBL. **Non-native. Ottawa County record.** Otherwise known in the state from Adair and Cherokee counties; sporadic occurrences in AR, KS, and MO. Voucher: *C. Curran 339 et al.*

Ranunculaceae (Buttercup family)

Clematis pitcheri Torr. & Gray var. *pitcheri.* Bluebill. FACU*, FAC

Enemion biternatum Raf. Eastern false rue-anemone. UPL, FACW. **Ottawa County record.** Common regionally, especially to the north and east, and known in most adjacent counties. Voucher: *N. Snow 10972 et al.*

Ranunculus abortivus L. Kidney-leaf buttercup. FAC, FACW

Ranunculus bulbosis L. vel aff. St. Anthony's turnip. UPL*, FACW. **Non-native.** Because of the uncertainty of its identification it is not included in the numerical tallies. However, if correct, it would represent a state record for Oklahoma. The nearest collections are from Cherokee County (KS) and Crawford County (AR). Voucher: *K. Stoehr 243 & S. Young*

Ranunculus fascicularis Muhl. ex Bigelow. Early buttercup. FACU, FAC.

Ranunculus hispidus Michx. var. *hispidus*. Bristly buttercup. FAC, FACW. **Ottawa County record.** Reported from counties due east and north and common regionally to the east; only two previous reports for OK (Logan and Muskogee counties). As of this time, eight collections in the Vascular Plant Data Base from Ottawa County of this species do not indicate an infraspecific level of identification. Voucher: *K. Stoehr 152 et al.*

Ranunculus hispidus Michx. var. *nitidus* (Chapman) T. Duncan. FACW, OBL

Ranunculus laxicaulis (Torr. & Gray) Darby. Mississippi buttercup. OBL. **Ottawa County record.** Reported for thirteen counties in eastern OK, Ottawa being the northern-most; widespread to areas north and (especially) southeast. Voucher: *C. Curran 58 & S. Young*

Ranunculus parviflorus L. Small-flowered buttercup. FACU, FAC. **Non-native. Ottawa County record.** Known relatively nearby from Jasper and Barry counties (MO) and nine counties in OK, the nearest being Rogers County. Voucher: *K. Stoehr 242 & S. Young*

Ranunculus pusillus Poir. Low spleenwort. FACW+, OBL

Ranunculus sardous Crantz. Hairy buttercup. UPL, FAC+. **Ottawa County record.** Reported extensively in AR and from several counties in eastern OK; closest in OK is Delaware County to the south and adjacent (to east) Newton County, MO. Voucher: *K. Stoehr 270 et al.*

Ranunculus scleratus L. *var. scleratus*. Cursed buttercup. OBL. **Ottawa County record.** Widespread across the southern Great Plains and areas east; the nearest collections from Cherokee County (KS) and Mayes County in OK. Vouchers: *N. Snow 10847 et al.*; *K. Stoehr 74 et al.*

Rosaceae (Rose family)

Crataegus crus-galli L. Cock-spur hawthorn. FACU, FAC

Crataegus phaenopyrum (L. f.) Medik. Washington Hawthorn. FAC-, FAC. **Oklahoma state record.** Native from Missouri and Arkansas (where extirprated) east to Florida and Connecticut (Kartesz 2017). The nearest known collection is Japser County (MO). Voucher: *Stoehr 220 & S. Young*

Crataegus viridis L. var. *viridis*. Green hawthorn. FACU+, OBL

Geum vernum (Raf.) Torr. & Gray. Spring avens. FACU-, FAC

Potentilla recta L. Sulfur cinquefoil. **Non-native.** Unranked

Potentilla simplex Michx. Oldfield cinquefoil. UPL, FACU

Prunus hortulana Bailey. Hortulan plum. Not ranked.

Prunus serotina Ehrh. var. *serotina*. Black cherry. FACU

Prunus virginiana L. Chokecherry. UPL, FAC. **Ottawa County record.** Known from eight counties in OK, the closest in OK being either Adair (south) or Rogers (southwest) counties, and Labette County (KS) slightly to the northwest; the species is widespread across much of northern and western parts of the U.S.A. and adjacent parts of Canada. Voucher: *N. Snow 10964 & C. Curran*

Pyrus calleryana Dcne. Bradford pear. Unranked. **Non-native. Ottawa County record.** This widely planted flowering tree has become established in many areas of the eastern US and western US. Its nearest record is Jasper County (MO) to the east. Voucher: *N. Snow 10960 & S. Young*

Rosa multiflora Thunb. Rambler rose. UPL, FACU. **Non-native**

Rosa setigera Michx. Climbing rose. FACU-, FACU+

Rubus spp. See above regarding identification of species in this genus. Species reported for Ottawa County (Kartesz 2017; ONHI 2017) but not confirmed by our work include: *Rubus aboriginum*

Rydb., *Rubus allegheniensis* Porter var. *allegheniensis*, *R. bushii* Bailey, *R. flagellaris* Willd., *R. mollier* Bailey, *R. occidentalis* L., and *R. ostryafolius* Rydb. The lattermost is reported by ONHI (2017) for Ottawa county, but the taxonomic concept of Kartesz (2017) restricts that taxon to a narrow distribution in Maryland, Delaware, and possibly into Virginia and as far north as Maine. One specimen tentatively identified as *R. bifrons* Vest (*Sperry Herbarium Staff 412*) would be a county record of a non-native but aggressively weedy species ("Himalayan blackberry"), although its invasive tendencies are strongest in the Pacific Northwest, where it designated as a noxious weed in Washington and Oregon.

Rubiaceae (Madder family)
Cephalanthus occidentalis L. Common buttonbrush. OBL.
Cruciata pedemontana L. Piedmont bedstraw. Unranked. **Non-native**
Diodia teres Walt. Poorjoe. UPL, FACU
Galium aparine L. Sticky-willy. FACU, FAC-
Galium pilosum Ait. Hairy bedstraw. Unranked
Galium sherardia Krause. Blue field-madder. Unranked. **Non-native. Ottawa County record.** Reported for much of eastern OK, most of AR, and a few counties relatively nearby in KS and MO. Voucher: *C. Curran 75 & S. Young*
Galium tinctorium (L.) Scop. Stiff marsh bedstraw. FACW, OBL
Galium triflorum Michx. Flagrant bedstraw. FACU, FACU+. **Ottawa County record.** Reported for approximately fifteen counties in OK and known from all counties adjacent to Ottawa County. Voucher: *C. Curran 296 & S. Young*
Houstonia pusilla Schoep. Tiny bluet. UPLP*, FAC-
Spermacoce glabra Michx. Smooth false buttonwood. FACW, FACW+

Salicaceae (Willow family)
Populus deltoides Bartr. ex Marsh. subsp. *deltoides.* Eastern cottonwood. FAC, FACW*
Salix caroliniana Michx. Carolina willow. FACW+, OBL
Salix nigra Marsh. Black willow. FACW+, OBL

Santalaceae (Sandalwood family)
Phoradendron leucarpum (Raf.) Reveal & M.C. Johnston subsp. *leucarpum.* Oak mistletoe. Unranked (parasitic ephiphyte). **Ottawa County record.** Reported for over half the counties in eastern OK, the nearest being Craig and Nowata counties; also known (rare) in adjacent Cherokee County (KS). Voucher: *C. Curran 14 & N. Snow*

Scrophulariaceae (Figwort family)
Verbascum blattaria L. White moth mullein. UPL, FAC. **Non-native**

Smilacaceae (Greenbriar family)
Smilax bona-nox L. var. *bona-nox.* Fringed greenbriar. FACU, FAC
Smilax hispida Muhl. ex Torr. Chinaroot. FAC, FAC+
Smilax lasioneuron Hook. Blue-ridge carrion flower. Unranked
Smilax rotundifolia L. Horsebriar. FAC

Solanaceae (Potato family)
Datura stramonium L. Jimsonweed. Unranked. **Non-native**
Physalis angulata L. Cut-leaf ground-cherry. UPL, FAC
Physalis cordata P. Mill. Heart-leaf ground-cherry. Unranked. **Ottawa County record.** Reported for Pushmataha and Choctaw counties in OK, with the nearest record in Barry County, MO. Voucher: *C. Curran 220 & S. Young*

Physalis longifolia Nutt. var. *longifolia*. Long-leaf ground-cherry. Unranked
Physalis longifolia Nutt. var. *subglabrata* (Mackenzie & Bush) Cronq. Unranked
Solanum carolinense L. *var. carolinense*. Carolina horse-nettle. UPL, FACU. **Non-native. Noxious.**
Solanum elaeagnifolium Cav. Silver-leaf nightshade. Unranked. **Ottawa County record. Noxious.**
    Known across Oklahoma and most nearby counties in adjacent states (AR, KS, MO). Voucher:
       Sperry Herbarium Staff 440
Solanum ptychanthum Dunal. Eastern black nightshade. Unranked.

Ulmaceae (Elm family)
Ulmus alata Michx. Winged elm. FACU, FACU+
Ulmus americana L. American elm. FAC, FACW
Ulmus rubra Muhl. Slippery elm. FAC-, FAC

Urticaceae (Nettle family)
Boehmeria cylindrica (L.) Sw. Small-spike false nettle. FACW, OBL
Laportea canadensis (L.) Weddell. Canadian wood-nettle. FAC, FACW
Parietaria pensylvanica Muhl. ex Willd. Pennsylvania pellitory. FACU-, FACW-
Pilea pumila (L.) Gray. Canadian clearweed. FAC, FACW

Valerianaceae (Valerian family)
Valerianella radiata (L.) Dufr. Beaked cornsalad. FACU*, FACW

Verbenaceae (Verbena family)
Glandularia canadensis (L.) Nutt. Rose mock-vervain. Unranked
Phyla lanceolata (Michx.) Greene. Northern frogfruit. FACW, OBL
Verbena hastata L. Simpler's joy. FAC, FACW+
Verbena urticifolia L. White vervain. UPL, FAC+

Violaceae (Violet family)
Viola bicolor Pursh. Field pansy. UPL, FAC
Viola missouriensis Greene. Missouri violet. FACU*, FACW+
Viola nephrophylla Greene. Northern bog violet. FACU, FACW+
Viola pubescens Ait. Downy yellow violet. FACU-, FACW
Viola sororia Willd. Hooded blue violet. FAC*, FAC

Vitaceae (Grape family)
Ampelopsis cordata Michx. Heart-leaf peppervine. UPL, FAC+
Parthenocissus quinquefolia (L.) Planch. Virginia-creeper. FACU, FAC
Vitis aestivalis Michx. var. *lincecumii* (Buckl.) Munson. Summer grape. UPL, FAC
Vitis cinerea (Englem.) Engelm. ex Millard var. *cinerea*. Gray-bark grape. FAC, FACW

ADDITIONS AND COMMENTS ON THE VASCULAR FLORA
OF CADDO PARISH, LOUISIANA

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ABSTRACT
The vascular flora of Caddo Parish, Louisiana, is updated. Field research has yielded two new species, one previously reported but now ubiquitous species, and one problematic species.

Since the publication of our "An updated, annotated vascular flora of Caddo Parish, Louisiana, with notes on regional phytogeography and ecology" (MacRoberts & MacRoberts 2006) and several updates recording new species to the parish (MacRoberts et al. 2012, and references), we have continued to locate interesting additions. Two new additions are reported and one problematic and one interesting species are discussed. The Caddo Parish vascular plant list now stands at 1443 species, of which about 17% are non-native.

APIACEAE
Bowlesia incana Ruiz & Pavon, *MacRoberts & MacRoberts 8975, 8976, 8989* LSUS; *8977, 8988* LSU. We reported this species for Caddo Parish (MacRoberts & MacRoberts 2006) on the basis of a R. Dale Thomas specimen collected in the late 1990s and housed at NLU. Except for the Thomas specimen, *Bowlesia incana* had not been previously reported for northwest Louisiana, southern Arkansas, or northeast Texas (Kartesz 2014; Turner et al. 2003). Recently we found this species to be ubiquitous in frequently mowed areas in Shreveport parks, along highways, LSU-Shreveport campus, and in other locations around the city. Because *Bowlesia incana* is now so common in Shreveport, we decided to see if it was common elsewhere. A few short trips settled the matter; we found it abundant near the Shreveport-Barksdale Bridge in Bossier City, Bossier Parish, and it is abundant in frequently mowed roadside parks in Shelby and Harrison counties, Texas (*MacRoberts & MacRoberts 8990, 8991*, LSU, LSUS, TEX).

COMMELINACEAE
Murdannia nudiflora (L.) Brenan, *MacRoberts & MacRoberts 8959* US; *8960* LSU. While the Louisiana Commelinaceae was of special interest to D.T. MacRoberts (1980), he never found *Murdannia nudiflora,* and it has not otherwise been reported from northwest Louisiana or northeast Texas, with only one county record for southeast Arkansas (Kartesz 2014). We found it to be common along a 300 meter intermittent stream in Columbia Park, Shreveport. It was first located in 2014 and has persisted at least until 2016.

HYDROPHYLLACEAE
Nemophila aphylla (L.) Brummitt, *MacRoberts & MacRoberts* 8981 LSU. This species has been reported widely distributed across Louisiana, southeast Texas, and Arkansas but not for Caddo Parish (Kartesz 2014). We discovered two plants in Columbia Park, Shreveport. While additional searches were made, no other sites were found.

SALVINIACEAE
Salvinia sp., MacRoberts and MacRoberts 8972, 8973 LSU, LSUS. (Figure 1). The taxonomy of *Salvinia* appears to be controversial. There is much confusion and discourse surrounding *S. minima*

Baker and *S. molesta* D.S. Mitch. We have been observing *Salvinia* in Bickham-Dickson Park, Shreveport (MacRoberts et al. 2008) since the heavy and extended floods of 2016 (it was not present there in 2008). All keys that we have consulted lead to confusion, because all of the specimens we have found (and raised in tubs) show characteristics of both *S. minima* and *S. molesta* as described in available keys. Thus while all of our collections have "egg beater" hairs on the upper surface of the leaf, the floating leaves are small (6-15mm long), not folded, and their lower surface is more or less densely covered with long hairs (see key in Diggs and Lipscomb 2014). Conversations with local "experts" and a summary of the literature have not led to an unambiguous determination; there is talk of sterile plants, hybrids, age grades, and so on. In any case, whatever this small-leaf *Salvinia* is, it is common in Bickham-Dickson Park. *Salvinia molesta* has previously been reported from Caddo Parish (Kartesz 2014).

Figure 1. *Salvinia* at Lake Martin (Lake la Pointe), St. Martin Parish, Louisiana (photo by Bill Wood).

ACKNOWLEDGMENTS

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GREEN/RED AND WHITE ASHES (*FRAXINUS* SECT. *MELIOIDES*) OF EAST-CENTRAL NORTH AMERICA: TAXONOMIC CONCEPTS AND POLYPLOIDY

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ABSTRACT

Taxonomic problems among the green/red and white ashes (*Fraxinus* sect. *Melioides*) of east-central North America are reviewed. Within green/red ashes (*F. pennsylvanica* sensu lato), a distinction is made between largely southern/eastern plants (referable to var. *subintegerrima* and var. *pennsylvanica**) and largely northern/western plants (probably referable to var. *campestris* and var. *austinii**). The latter include the common cultivar "Marshall's Seedless." They tend to have smaller leaves, shorter petiolules, more leaflet serration, larger buds relative to leaf scars, and smaller samaras. Within both groups, relatively pubescent variants (*) tend to have larger samaras and may also be usefully segregated. It has been generally assumed that pumpkin ash (*F. profunda*) is a distinct hexaploid species, but there is only one reported chromosome count, and even with fruits there is uncertainty in distinguishing some collections from *F. pennsylvanica*. White ashes have been interpreted by Nesom in 2010 as a polyploid series (*americana* = 2x, *smallii* = 4x, *biltmoreana* = 6x), based largely on cytological studies during 1947–1983, but there have been few reliable chromosome-counts indicating polyploids and these lack supporting collections. Recent results from flow cytometry with plants referable to *F. smallii* indicate only hexaploids. Relatively reliable reports of tetraploids are more restricted to southern regions than indicated by Nesom. The only obvious difference between *F. smallii* and *F. biltmoreana* is that the latter is more densely pubescent, especially on rachises and young twigs. It is suggested that most plants referable to *F. smallii* should be treated as **F. biltmoreana** var. **subcoriacea**, J.J.N. Campbell, **comb. nov.** Diploid *F. americana* (sensu stricto) remains variable in pubescence and in samara size, which displays a bimodal tendency, but there is no obvious basis yet for recognition of further segregates. This taxonomic scheme is supported by keys, state-distribution maps, principal components analysis of morphometric data from 160 collections, and patterns in frequency distributions of samara sizes.

During recent decades, most ashes (*Fraxinus*) in east-central North America—centered on the Ohio River watershed—have generally been referred to three species: blue ash (*F. quadrangulata*), green or red ash (*F. pennsylvanica*) and white ash (*F. americana*). While it is generally agreed that blue ash is relatively uniform, variants within the other species have been recognized or rejected in somewhat inconsistent fashion by botanists, foresters, and horticulturalists (e.g., Little 1952; Miller 1955; Gleason & Cronquist 1991; Burns & Honkala 1990; Dirr 1997; Ward 2011). Distinction between green/red ash and white ash is considered difficult enough in some cases, and different treatments of segregates within each of these species have tended to confuse the situation further. There has, however, been a resurgence of interest in these problems given Nesom's (2010a-f, 2014) recent review of the genus in North America, which recognized three species within *F. americana* sensu lato: typical *F. americana*, all diploid (2n = 46); *F. smallii*, reportedly tetraploid; and *F. biltmoreana*, reportedly hexaploid. Variation within the green/red ash complex has also been problematic. Morphological distinction of the supposed hexaploid *F. profunda* from diploid *F. pennsylvanica* is sometimes difficult, even with samaras. There is considerable remaining variation within *F. pennsylvanica*, although tetraploids have not been documented. The search for cryptic polyploid species within traditional "species" of vascular plant is a reasonable goal, given that such segregates tend to be reproductively isolated (e.g., Soltis et al. 2008).

The advent of Emerald Ash Borer, now devastating most ashes across northern sections of this region (Herms & McCullough 2014), now makes it urgent to resolve the taxonomic issues in defining ash species, to recognize meaningful intraspecific entities, and to document even local genetic variants. As well as the need for better assessment of native trees, it is important to determine what kinds of ash have been cultivated or planted in restoration projects. There will be an effort by the USDA to breed EAB-resistant ashes for future uses (Koch et al. 2012). The full diversity of native ash germplasm should obviously be sampled as part of this effort, avoiding potential confusion with cultivated material that has been widely distributed (Knight et al. 2010).

Most eastern species of *Fraxinus*—all except *F. nigra* and *F. quadrangulata*—belong in the largely North American sect. *Melioides* (Jeandroz et al. 1997; Wallander 2008; Hinsinger et al. 2013). This section has the following characteristics: plants dioecious, the flowers strictly unisexual, with persistent calyx, female with one pistil, male with two stamens; samaras with length/width usually 5–9, distinctly narrowed to little or no wing at base, the seed cavity usually terete; terminal buds apiculate or acute, often blackish but (at least on more exposed scales) proximally to completely covered with usually reddish-brown glands (sometimes orange, golden or purplish); leaflets 3–9, the terminal one usually at least as large as adjacent pair, the laterals on petiolules 0–15(20+) mm long, serrulate to subentire on flowering shoots, largely glabrous to densely pubescent below but without distinct basal tufts, the hairs stramineous to whitish, short and straight or long and slightly curling; young twigs when dried usually pale olive-greenish to brownish or purplish (especially at nodes), terete; trees up to 10–35 m tall. Plants have diverse flavones but lack coumarins, in marked contrast to sect. *Fraxinus* (Black-Schaefer & Beckmann 1989; Lee et al. 2012; Whitehill et al. 2012).

Sect. *Melioides* appears to contain two major subgroups (Nesom 2014): the Pennsylvanica group or "green / red ashes" and the Americana group or "white ashes." Hybrids between these groups are apparently rare to absent in the wild (Nesom 2010a-f; Ward 2011). Santamour (1962) reported one possible hybrid out of the 46 trees sampled ("NEG-789" from southern Indiana). Taylor (1972) found only one apparent wild hybrid during three years of study. Miller (1955) suggested that the following taxa originated from hybrids: (1) plants now known as *Fraxinus pauciflora* from *F. caroliniana* and *F. americana*; (2) *F. profunda* (as *F. tomentosa*) from *F. pennsylvanica*; and (3) *F. biltmoreana* (as a variety) from *F. americana* and *F. pennsylvanica*. However, no definitive evidence has emerged to support these three hypotheses (Black-Schaefer & Beckmann 1989; Hardin & Beckmann 1982; Nesom 2010f).

Hybrids between these two subgroups of sect. *Melioides* have been produced artificially (Taylor 1972; J. Koch, pers. comm.) and some cultivars are suggestive of hybrid origin. *Fraxinus americana* "Rosehill" has clear white-waxy reticulation between ultimate veinlets but the veinlets are relatively wide and remain bright green when dried. *Fraxinus pennsylvanica* (or *F. americana*) "Cimmaron" (or "Cimmzam") also has suggested hybrid origin (US Plant Patent 8077 in 1992 by J.W. Zampini). But, again, no definitive evidence of such hybridity in cultivars has been presented.

Within *Fraxinus pennsylvanica* as generally circumscribed, Miller (1955) and Nesom (2010c) did not recognize formal segregates, but Nesom noted the potential for further study to support variants. Britton (1908) had described *F. campestris*, centered in the northern Great Plains, and Peterson (1923) used this name for all green or red ash in Nebraska. Gates (1938) treated this taxon as *F. pennsylvanica* var. *campestris* (Britton) F.C. Gates (or "prairie ash"), and he provided maps of it as well as var. *subintegerrima* and var. *pennsylvanica* in Kansas. Britton (1908) and Small (1933) also distinguished *F. darlingtonii* Britt., based on its longer more linear samaras, smaller leaf blades with entire margins, less general twig pubescence, and more southern range. Fernald (1950) treated less pubescent plants as var. *subintegerrima*, apparently including *F. darlingtonii*, and he added var. *austinii* as a name for more pubescent plants with relatively short and broad samaras, more serrate

leaves, and relatively northern range. Gleason (1952) and Farrar (1995) also made useful comments on some of these variants.

Nesom (2010a) has recently improved knowledge of the enigmatic "pumpkin-ash"— *Fraxinus profunda* (= *F. tomentosa* and probably *F. michauxii*). This taxon has been interpreted as a hexaploid derivative from the *pennsylvanica* complex, usually with distinctively larger samaras and often with larger leaves. But variation within this species is poorly understood and is addressed further below.

Within *Fraxinus americana* sensu lato, Nesom's (2010f) recent division into three species (*americana, smallii, biltmoreana*) does concur somewhat with the treatments of Britton (1908), Sargent (1922), and Small (1933). Sargent's (1919) *F. americana* var. *subcoriacea* appears to be the same taxon as *F. smallii*. However, Fernald (1950) and Gleason (1952) recognized *biltmoreana* only as a more pubescent variety with relatively large samaras, centered in Appalachian to Ozark regions, and *F. smallii* has been generally not been recognized at all after Small (1933). Nesom's rationale was largely based on cytological work of Wright (1944a, 1957), Santamour (1962), Schaefer and Miksche (1977), Leser (1978), Armstrong and Funk (1980), Armstrong (1982), and Blake and Beckman (1983). Yet detailed review of this literature reveals some uncertainty in the supposed association of chromosome number with morphological features, as discussed below. And variation in samara size is considerable, even within each of Nesom's three species. Some authors (e.g., Fernald 1950) have recognized plants with unusually small samaras as *F. americana* var. *microcarpa* Gray (= var. *curtisii* (Vasey) Small), but there has been no quantitative assessment of variation in samara size.

In summary, this study is an investigation of green/red ashes (*Fraxinus pennsylvanica* sensu lato) and white ashes (*F. americana* sensu lato) in east-central North America. The distribution of each potential taxon is outlined. Confusion among some common cultivars and wild plants is addressed, with recognition of "Marshall's Seedless" and similar native plants as a distinct variety of *F. pennsylvanica* that has a relatively northwestern range. Within the *F. americana* complex, a transect of collections across central Kentucky transect is reported, with estimates of ploidy from flow cytometry. A modified version of Nesom's (2010a-f, 2014) treatment is developed, with a brief key (a) plus a more detailed version (b). Authors for names are listed in key (b) and not repeated elsewhere in the text; see Wallander (2008) for authors of other taxa. The more southern *F. caroliniana* complex is left for a subsequent paper.

Supplementary material is posted at bluegrasswoodland.com, including an extended report with details of samara size distributions and their statistics (Campbell 2017). Also posted at that website are selected images of all recognized taxa (Campbell 2015), and a provisional analysis of differences in habitat between ash taxa (Campbell 2011).

METHODS
Herbarium survey

Specimens were examined at several herbaria to improve understanding of the green/red ash and white ash complexes, based on visible characters of stems, leaves, and fruits. References below to these herbaria use standard acronyms (Thiers 2014). Characters in the existing keys of Fernald (1950), Gleason and Cronquist (1991), Nesom (2010a-f), and Weakley (2015) were used initially to review identifications. But more precise keys were developed, with elaboration or rejection of some characters where difficulties were encountered. Many specimens lack mature samaras, limiting their utility in taxonomic descriptions. Identification of such material remains problematic in some cases, despite efforts to refine descriptions of key characters. To explore variation in samara production, the percentages of specimens with samaras were determined for each suggested taxon at each herbarium. Provisional distribution maps were assembled for each suggested taxon, showing presence/absence in

each state or Canadian province. Images of selected herbarium specimens and living plants were assembled to illustrate characteristics of each taxon, but presented elsewhere (Campbell 2015).

For insight to covariance among visible morphometric characters in herbaria, an exploratory principal components analysis (PCA) was conducted with data taken from 160 collections at US during 23-26th Nov 2014. It is anticipated that a more extensive and rigorous morphometric analysis will be performed in the future, in order to test for correlations with DNA-based phylogenetic divisions. This initial analysis just establishes general patterns for development of future hypotheses. In *Fraxinus profunda*, *F.* cf. *smallii*, and *F. biltmoreana*, all collections with well-formed samaras were recorded. In *F. pennsylvanica* variants and *F. americana* (sensu stricto), only one random collection per state was recorded. The 15 scored characters are listed in Table 2. Within each collection, an average leaf and an average samara were subjectively selected for measurement. Quantitative characters were log-transformed, and then all characters were converted to a scale of 0 (minimum value) to 1 (maximum value). Data were analyzed using the PCA routine available online in R code (Revelle 2010; Wessa 2014).

Ploidy estimation

A transect across central Kentucky was driven on 21st Sep 2011 in order to collect fresh samples of the *americana-smallii-biltmoreana* complex for flow cytometry and for herbarium collections at NA. Within each of the seven counties crossed, an effort was made to find and collect each of the three suggested taxa along roadsides, resulting in a total of 24 collections. Leaf tissue for analysis was refrigerated, shipped overnight to the National Arboretum, and then analyzed with flow cytometry 2-3 days after arrival.

Flow cytometry was carried out by Craig Carlson under supervision of R.T. Olsen at the USDA, Beltsville, Maryland, on a Partec PA II flow cytometer using the Partec CyStain UV precise P kit (Partec GmbH, Münster, Germany) according to the manufacturer's instructions. Fresh leaf tissue of *Pisum sativum* 'Citrad', with absolute 2C = 8.75 pg, was used as the internal standard based on its common use as a reference standard (Doležel and Greilhuber 2010). [2C-value = nuclear DNA content of the whole chromosome complement that is characteristic for the organism.] Approximately 0.5 cm^2 of *Fraxinus* tissue was co-chopped with leaf tissue of the internal standard (<0.5 cm^2) using a double-sided razor blade in 400 µL of extraction buffer. Suspensions were filtered through 30-µm nylon mesh filters, and nuclei were stained with 1.6 mL of staining buffer containing 4',6-diamidino-2-phenylindole (DAPI). The nuclear suspension was analyzed on the flow cytometer with fluorescence excitation provided by a mercury arc lamp. The mean fluorescence of each sample was compared to that a known diploid with 46 chromosomes, and to the internal standard for determination of relative ploidy level and holoploid genome size, respectively. At least 3000 nuclei were counted for determining the ratio of sample peak to the internal standard, and thus nuclear DNA content: 2C pg = [sample peak/internal standard peak] × 8.75 pg.

RESULTS

Current taxonomic rationale and new combination for *Fraxinus smallii*

As detailed below, typical pubescent *Fraxinus biltmoreana* is often mixed with more glabrous plants in populations, and there is little obvious ecological difference between pubescent and glabrous plants in Kentucky. Thus *F. smallii* may be regarded merely a less pubescent variant of hexaploid *F. biltmoreana*, with some geographic segregation but no discontinuity. Formal taxonomic recognition of the less pubescent form may have little evolutionary significance, but it is adopted here with the following provisional name, under which to organize observations. This allows some internal consistency between nomenclature for the *F. americana* complex and for *F. pennsylvanica*, which also has pubescent-versus-glabrous varieties. The nomenclature adopted here for varieties of *F. pennsylvanica* is provisional as well, partly since more checking of all potentially relevant types is needed to be sure of their appropriate application.

FRAXINUS BILTMOREANA Beadle var. SUBCORIACEA (Sargent) J.J.N. Campbell, **comb. nov.**
Fraxinus americana var. subcoriacea Sargent, Bot. Gaz. 67: 241. 1919. SYNTYPES: **USA**.
Massachussetts. Suffolk Co.: Boston, cultivated at the Arnold Arboretum in Jamaica Plain,
10 Oct 1905, collector not specified (AA 283679!, AA 73800!).
Fraxinus smallii Britton, N. Amer. Trees, 805, f. 735. 1908. TYPE: **USA. Georgia**. Gwinnett Co.:
Yellow River near McGuire's Mill, 750 ft, 2 Aug 1895, *J.K. Small s.n.* (holotype: NY!;
isotype: GH!).

Notes on characters for identification of taxa

The white waxy "papillose" or "corniculate" reticulation of Couplet 1 below is a diagnostic character of white ashes (Miller 1955; Hardin & Beckman 1982; Nesom 2010f; Williams & Nesom 2010). However, it can be difficult to assess even when viewed with at least ×40 magnification, as recommended here. The character is not generally apparent in seedlings a few years old, as noted by Taylor (1972). It is also less developed in immature leaves or in deep shade, and it may become less apparent after hotter drying. Identification of seedlings and shade leaves as white ashes (*Fraxinus americana* sensu lato) versus green/red ashes (*F. pennsylvanica* sensu lato) may still be possible from examination of lower leaflet surfaces, but more definitive analysis is needed. In white ashes from forest understories, the areolae appear to have a relatively uniform pale green to bluish-white (or 'silvery') waxy covering with fine texture (granules < apparent cell width). The fine veinlets are usually pale green with an exposed width of up to ca. 0.05 mm. In green/red ashes from the understory, lower leaflet surfaces are generally deeper green than the white ashes, and the areolae appear less uniform in color, with small patches (perhaps cells) of yellow-green to orange-brown (or 'golden') and white (perhaps waxy cells). Fine veinlets of green/red ashes appear up to ca. 0.1 mm wide and are usually deeper yellowish- or brownish-green. Relatively large, distinct, orange-brownish "peltate glands" or "scales" often appear scattered to frequent in the green/red ashes, usually near the centers of areolae. Hardin and Beckmann (1982) reported no clear differences in frequency of such "scales" between white and green/red ashes, but in the white ashes these structures tend to be obscured by the more uniform waxy surface. Stomata can also appear relatively dense or clustered in green/red ash (Taylor 1972).

Stomata, leaflet shape, petiolules, buds, twigs and wood anatomy all need more study in shade versus sun, on mature branches versus or juvenile leaves, and on slow versus fast-growing shoots, in order to determine how taxonomically useful their variation might be. White ashes usually have leaf bases 'trunctate to rounded' with angles of 45–90°; green/red ashes usually have 'cuneate to acute' bases with angles of 30–45°, but often up to 60° in *Fraxinus profunda*. Petiolule length has some value, but there is overlap; Steyermark (1963) used "3–20 mm" in *F. americana* (sensu lato), versus "1–5(9) mm" in *F. pennsylvanica*. Other characters were suggested by Taylor (1972) but based only on typical *F. americana* versus typical *F. pennsylvanica* in Michigan. She noted as follows: that *F. americana* has bud scars more angled out from the twig surface (ca. 20–30° versus 10–20°) and strictly opposite (versus often subopposite); that twig surfaces in second year are usually greenish to purplish (versus grayish), with waxy exfoliation (versus not so); that bark remains smooth for many years and strictly gray to blackish (versus soon becoming corky in later years and often olive- to reddish-brown); and that styles are red to purple (versus greenish). She reported that bud-scar and twig characters are most distinctive on shoots growing at ca. 3–6 cm per year.

Within the green/red ash complex, there are some statistical differences in mean leaf and leaflet dimensions between taxa, based on collections at US, and these are used in the keys below. In particular, mean terminal leaflet width (± standard error) in *Fraxinus pennsylvanica* var. *subintegerrima* is 3.96 ±0.16 cm (n = 20); it is 4.50 ±0.21 cm (n = 16) in var. *pennsylvanica* (P = 0.046 with T test). However, there is no significant difference in petiolule length. *F. profunda* has generally larger leaf dimensions, including a strong difference in petiolule length: 5.94 ±0.64 mm (n

= 18) versus 3.18 ±0.27 mm in south/eastern variants of *F. pennsylvanica* (n = 36); P <0.0001 with T test. But there is again some overlapping variation within both of these species.

Pubescence of lower leaf surfaces varies too much across ranges of whole species to be a reliable character in most taxonomic distinctions. But some useful observations can be derived from local populations. Within Kentucky, *Fraxinus americana* (sensu stricto) is usually glabrous except on larger veins and it rarely if ever has dense hairs across the surface, while *F. biltmoreana* (including *F. smallii*) usually has widespread hairs that are often dense across the surface. Within *F. americana* (sensu stricto) pubescence appears generally denser in states to the west and south of Kentucky, as also indicated by Wright (1944a). However, within *smallii*-like plants pubescence appears generally less dense in states to the west and perhaps south of Kentucky.

Although samara size and shape are useful characters in several parts of the key, it is important not to overstate their value, given the initial analysis of variation in overall size presented elsewhere (Campbell 2017). Variation in anther size and shape remains largely unexplored; Fernald (1950) made a few notes on anthers but no general survey of taxa has been reported.

(a) Brief version of the key (for inital use to estimate identifications)

1. Lower leaflet surface not whitish waxy-papillose-reticulate or bluish-silvery [viewed at ×40]; samara wings decurrent to 20–100% below apex of bodies, these with L/W [length/width] ca. 5.5–12

    2. Leaflets mostly 7.5–11× 2.5–5 cm with petiolules 1–5 mm; samaras mostly 25–50 × 3–8 mm, the bodies 12–22 × 1–2.5 mm, yellowish to brown

        3. Leaves on fertile shoots averaging 15–20 cm long; lateral leaflets with petiolules mostly 1.5–3 mm, distinctly serrate; lateral buds mostly 50–150% as wide as leaf scar; samaras with L/W mostly 5.5–8

            4. Leaves and fresh stems largely glabrous; samaras mostly 25–40 × 3.5–6 mm
.... **Fraxinus pennsylvanica** var. **campestris**
            4. Leaves and fresh stems densely pubescent; samaras mostly 30–45 × 4–8 mm
.... **Fraxinus pennsylvanica** var. **austinii**

        3. Leaves on fertile shoots averaging 20–25 cm long; lateral leaflets with petiolules mostly 3–5 mm long, entire to weakly serrate; lateral buds mostly 30–90% as wide as leaf scars; samaras with L/W mostly 7–11

            5. Fresh twigs, rachises and lower leaflets surfaces largely glabrous; leaflets often weakly serrate
.... **Fraxinus pennsylvanica** var. **subintegerrima**
            5. Fresh twigs, rachises and lower leaflets surfaces densely pubescent; leaflets usually subentire
.... **Fraxinus pennsylvanica** var. **pennsylvanica**

    2. Leaflets mostly 9–15 × 3.5–7 cm with petiolules 4–14 mm; samaras mostly 42–65 × 6–11 mm, the bodies 18–30 × 2.5–4.5 mm, often reddish .... **Fraxinus profunda**

1. Lower leaflet surface whitish waxy-papillose-reticulate or bluish-silvery, at least between veinlets [less clear in juvenile or shade leaves]; samara wings decurrent to 10–30% below apex of bodies, these with L/W ca. 4–5.5

    6. Petiole bases deeply notched around buds, the margins sharp; rachises and fresh twigs usually glabrous; samaras mostly 25–37.5 × 3–5.5 mm, the bodies 6–11 × 1.5–2.5 mm [some northern populations have samaras 35–45 mm long] .... **Fraxinus americana** (sensu stricto)

    6. Petiole bases unnotched to slightly notched around buds, the margins blunt; rachises and fresh twigs densely pubescent to almost glabrous; samaras mostly 30–50 × 5–7 mm, the bodies 10–15 × 2–4 mm

7. Rachises and fresh twigs largely glabrous; leaflets subentire to weakly serrulate
.... **Fraxinus biltmoreana** var. **subcoriacea**
7. Rachises and fresh twigs usually covered with dense minute hairs; leaflets subentire
.... **Fraxinus biltmoreana** var. **biltmoreana**

(b) More detailed version of the key (for deeper examination and checking of identifications)

1. Lower leaflet surfaces green, without whitish minutely waxy-papillose reticulation or uniformly fine-textured bluish-silvery appearance [viewed at ×40], with complex texture [mosaic of cells and glands] and diverse colors from whitish to green to yellowish-brown [especially glands and veinlets], the ultimate veinlets usually prominent; upper surfaces darker than lower but both usually deep green to [especially in herbaria] dull orange-brownish or reddish green; leaves turning yellowish or orange-brown in fall, their hairs often slightly yellowish to reddish; leaflets often subsessile or with winged petiolules only 1–5 mm long [except in *profunda*], their shape and serration varied; bud scars with little [0–20%] or no notch; terminal buds brown to reddish-brown, usually acute and longer than wide, often narrower than twig when viewed on edge; twigs without flaking waxy surface; wing of samaras decurrent to ca. 20–100% below apex of body and gradually narrowed, usually acute at apex, the mature bodies [enclosing seeds] with L/W ca. 5.5–12, often distinctly ridged
.... **Pennsylvanica group**

2. Leaflets mostly 7.5–11× 2.5–5 cm [L × W 30–70 cm^2], usually cuneate, the petiolules (0)1–5(9) mm [distal pair]; pubescence largely absent or widespread on fresh twigs and leaves; female flowers with calyx 0.5–2(2.5) mm long; anthers with apiculate tip 0.2–0.4 mm long; samaras 25–50(60) × 3–8(11) mm, the wing decurrent to 20–50% below apex of body, the apex usually rounded to slightly emarginate [with notch rarely 1 mm deep], the mature bodies usually 12–22 × 1–2.5 mm, not plump [with distinctive ridges and channels], pale yellowish-brown to dark brown but rarely reddish

3. Leaves on fertile shoots usually averaging 15–20 cm long; lateral leaflets with petiolules (0.5)1.5–3(4) mm [rachis to inflexion], numbering 4–6(8), distinctly serrate [teeth mostly 0.4–0.8 mm deep], often with concentration of denser or longer hairs at base; terminal leaflet blades mostly 6–12 cm long, about as large as adjacent laterals; well-developed lateral buds mostly 50–150% as wide as leaf scar; samaras mostly 25–45 × 3.5–8 mm wide, with L/W 5.5–8, often oblanceolate to spathulate

4. Leaves and fresh stems largely glabrous except along midrib on lower leaf surface; samaras mostly 25–40 × 3.5–6 mm [or longer to east], L × W mostly 110–220 mm^2
.... **F. pennsylvanica** Marsh. var. **campestris** (Britt.) F.C. Gates
4. Leaves and fresh stems densely pubescent; samaras mostly 30–45 × 4–8 mm [or sometimes longer to east], L × W mostly 150–330 mm^2
.... **F. pennsylvanica** Marsh. var. **austinii** Fern.

3. Leaves on fertile shoots usually averaging 20–25 cm long; lateral leaflets with petiolules (2)3–5(9) mm long, numbering 6–8, entire to weakly serrate [teeth mostly 0–0.4 mm deep], without distinct concentration of hairs at base; terminal leaflet blades mostly 8–15 cm long, distinctly larger than adjacent laterals; well-developed lateral buds mostly 30–90% as wide as leaf scars; samaras mostly 30–50 × 4–6 mm, with L/W 7–12, strictly linear-lanceolate

5. Fresh twigs, rachises and leaflets largely glabrous, except along midrib on lower leaflet surfaces; leaflets mostly 3.5–4.5 cm wide, often weakly serrate [especially those of vigorous sprouts]; samaras mostly 4–5 mm wide
.... **F. pennsylvanica** Marsh. var. **subintegerrima** (Vahl) Fern.
[= *F. lanceolata* Borkh., *F. viridis* Bosc]

5. Fresh twigs, rachises and lower leaflets surfaces densely pubescent; leaflets mostly 4–5 cm wide, usually subentire; samaras mostly 5–6 mm wide
.... **F. pennsylvanica** Marsh var. **pennsylvanica**

2. Leaflets mostly 9–15 × 3.5–7 cm [L × W 40–90 cm^2], usually truncate to rounded at base, the petiolules (3)4–14(20) mm [distal pair]; pubescence usually dense on fresh twigs, petioles and rachises [but sparse to absent in some plants], often also on lower leaflet surfaces; female flowers with calyx (1)2.5–5(7) mm long; anthers with slender terminal cusp 0.5–1 mm long; samaras (32)42–65(74) × (5.5)6–11(12) mm, wing decurrent to 50–100% below apex of body, apex usually emarginate [with notch often about 1 mm deep], the mature bodies usually 18–30 × 2.5–4.5 mm, plump [with less distinctive ridges and channels], pale to dark reddish-brown
.... **F. profunda** (Bush) Bush [= *F. michauxii* Britt., *F. tomentosa* Michx.]

1. Lower leaflet surfaces whitish to pale green, with dense minute [1–10 microns wide] waxy papillae and connecting ridges [especially mature leaves in sun] or [juvenile or shaded leaves] uniformly fine-textured bluish-silvery appearance [with pale yellowish-brown glands somewhat obscured by wax], at least between veinlets, the ultimate veinlets usually somewhat obscured; upper surfaces usually plain green to [especially in herbaria] olive or bluish; leaves turning golden yellow, pinkish, reddish or purplish in fall, their hairs usually whitish; leaflets truncate to rounded at base [versus gradually cuneate], with distinct largely unwinged petiolules 3–13 mm long, abruptly acuminate at apex, entire to crenulate; bud scars sometimes with deep notch [>20%]; terminal buds dark reddish-brown to blackish, mostly obtuse-deltoid [but apiculate], about as wide as twig; twigs often with flaking waxy surface [especially 2nd year]; wing of samara decurrent to ca. 10–30% below apex of body and often abruptly narrowed, usually blunt to emarginate at apex, the mature bodies [enclosing seeds] with L/W ca. 4–5.5, indistinctly ridged .... **Americana group**

6. Petiole bases deeply notched (mostly 30–50%) around buds, the margins often sharp; rachises and fresh twigs usually glabrous; lower leaflet surfaces usually with hairs restricted to midrib and proximal parts of primary veins, sometimes more widespread to dense; upper leaflet surfaces usually plain yellowish-green; mature samaras mostly 25–38 × 3–5.5 mm [or 38–45 × 5.5–7 mm in some more northern populations], the bodies mostly 6–11 × 1.5–2.5 mm
.... **F. americana** L. (sensu stricto)

6. Petiole bases slightly notched [mostly 0–20%] around buds, the margins usually blunt; rachises and fresh twigs densely pubescent to almost glabrous, lower leaflet surfaces usually with hairs dense along veins, often widespread over lower leaflet surfaces, sometimes thin to glabrous; upper leaflet surfaces usually somewhat bluish-green; mature samaras mostly 30–50 × 5–7 mm, the bodies mostly 10–15 × 2–4 mm.

7. Rachises and fresh twigs largely glabrous, sometimes irregularly or thinly hairy especially in distal parts of rachis; leaflets subentire to crenulate or weakly serrulate [as in *F. americana*] ....
.... **F. biltmoreana** Beadle var. **subcoriacea** (Sarg.) J.J.N. Campb.
[= *F. smallii* Britt.]
7. Rachises and fresh twigs usually covered with dense minute hairs, sometimes moderately dense to sparse but still uniform; leaflets usually subentire
.... **F. biltmoreana** Beadle var. **biltmoreana**
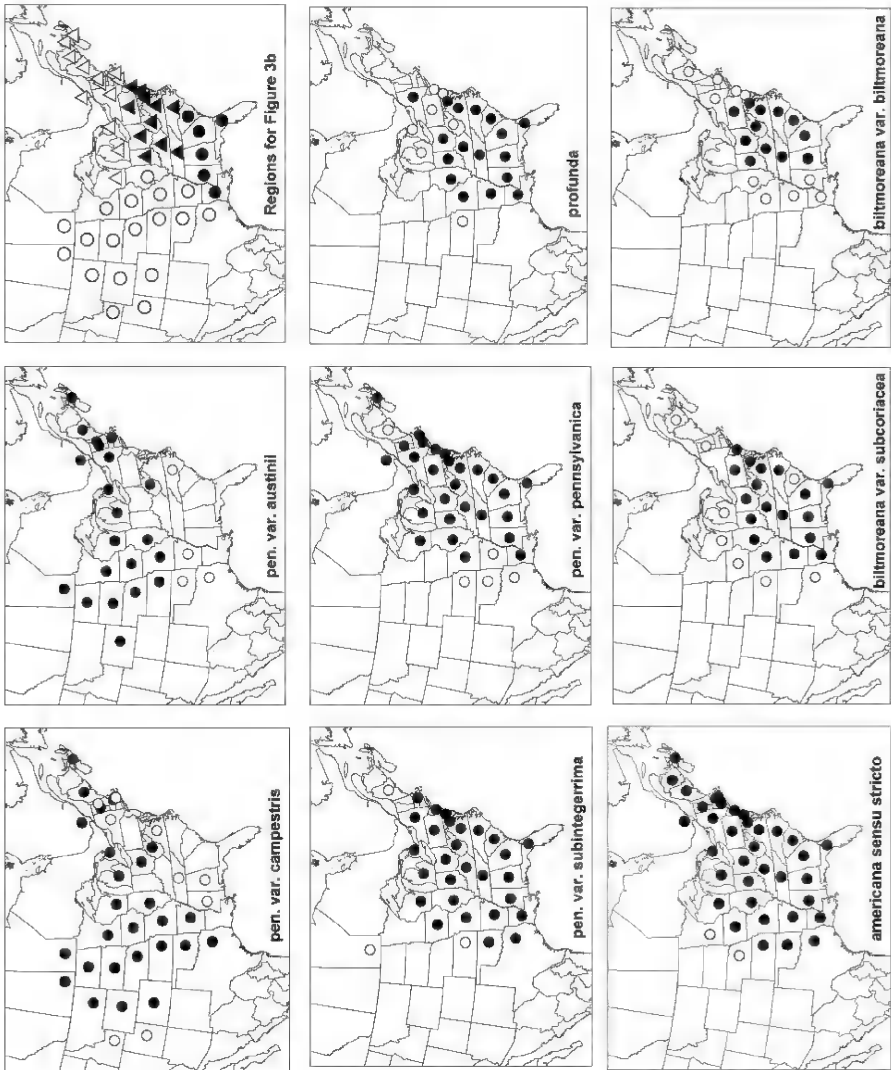[= *F. americana* L. var. *biltmoreana* (Beadle) J. Wright ex Fern.]

Figure 1 [previous page]. Distribution maps of *Fraxinus* taxa that are the focus of this study. These are provisional maps based largely on collections seen at APSC, AUA, FLAS, GA, MISS, MU, MUHW, NA, NY, TENN, US, VPI and WVU, plus records compiled by Nesom (2010a, c, f). Solid dots indicate that the taxon is reliably recorded with many typical collections. Open dots indicate that the taxon is uncommon (generally less than 10 counties), or that plants are not generally typical (perhaps intergrading with another taxon in some cases). Maps for *F. pennsylvanica* are divided into the four provisional variants (see key): var. *campestris* (informally "NW smooth"); var. *austinii* ("NW hairy"); var. *subintegerrima* ("SE smooth") and var. *pennsylvanica* ("SE hairy").
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Distribution maps

Figure 1 presents maps of each suggested taxon's native occurrence in states and Canadian provinces. In the green ash complex, the two northwestern variants have ranges that are distinct from the two southeastern variants, extending further into the Great Plains and largely absent from southeastern states. See Discussion for notes on new records of *F. profunda*. In the white ash complex, there are only a few minor additions to Nesom (2010f). There are *smallii*-like or *biltmoreana*-like collections as far north as Maine and New Brunswick, but these might just be unusual collections of *Fraxinus americana* without a distinct notch in the petiole base and bud scar.

Polyploidy

Table 1 lists the 24 collections from central Kentucky for estimation of ploidy using flow cytometry. Estimations were all diploid (2n = 46)—for the 14 collections determined as *Fraxinus americana*—or hexaploid (2n = 138)—for the 10 collections determined as *F. smallii* (5) or *F. biltmoreana* (5). Three collections of *F. americana* were initially misidentified as *F. smallii*, generally due to more obscure notching of petiole bases on vigorous shoots. No fruiting material was located during the survey. The proportion of *F. americana* collections tended to increase from south to north (M to K to B under "region"); P = 0.06 with chi-square test in 2 × 3 contingency table. The lack of tetraploids in central Kentucky is consistent with sampling by R. Olsen and A. Whittemore (pers. comm.) in mid-Atlantic states. [A much more extensive survey using flow cytometry is currently underway, and there will be efforts to correlate stomatal sizes with these results, as well as direct chromosome counts.]

Principal Components Analysis [PCA]

Despite the rudimentary nature of morphometric data used here, with only 15 characters (interdependent in some cases) and only 160 thinly sampled collections, there is a surprising degree of separation in the analysis between the provisional taxa (Figure 2). The first and second axes are sufficient to display all readily interpretable patterns in the data, accounting for 27% and 23% of the total sum-of-squares variance; in a trial with six axes the sequential percentages were 23, 20, 13, 10, 10 and 9. The first axis emphasizes dimensions of leaf size and, to a lesser extent, samara size; characters with opposing trends are leaf serration and narrow leaf shape (Table 2a). The second axis emphasizes samara size and pubescence, together with notched petioles and waxy-papillose leaf

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Table 1 [next page]. Determinations of ploidy with flow cytometry from collections of white ashes from central Kentucky. See text for key to identifications. Collections marked with asterisks (*) were initially identified as *F. smallii* (= *F. biltmoreana* var. *subcoriacea*) but closer examination, after results of flow cytometry, confirmed that they are better placed in *F. americana*. Collections that were from unusually vigorous sprouts are indicated under "sprout"; these were mostly along roads with occasional cutting. Under region: M = Mississippian Plateaus; K = Knobs and transitions; B = Bluegrass.

Table 1 [caption on previous page].

Identification	Ploidy	Number	Sprout	County	Region	Latitude	Longitude
americana	diploid	1b-i		Metcalfe	M	37.09239	-85.69832
americana	diploid	2c-i		Green	M	37.22714	-85.51380
americana	diploid	3a-i		Taylor	K	37.36717	-85.30770
americana	diploid	3b-i		Taylor	K	37.43954	-85.28601
*americana**	diploid	3b-ii		Taylor	K	37.44007	-85.28705
americana	diploid	4a-i		Marion	K	37.44836	-85.29196
americana	diploid	4c-i		Marion	K	37.57442	-85.15495
americana	diploid	5b-i	+	Boyle	B	37.68918	-84.92180
*americana**	diploid	6a-i	+	Mercer	B	37.70434	-84.89778
americana	diploid	6a-ii		Mercer	B	37.70429	-84.89856
americana	diploid	6b-i		Mercer	B	37.81660	-84.73783
americana	diploid	7a-i	+	Jessamine	B	37.86182	-84.70140
*americana**	diploid	7b-ii		Jessamine	B	37.86760	-84.69138
americana	diploid	7b-iii		Jessamine	B	37.86731	-84.69108
smallii	hexaploid	1a-i		Metcalfe	M	37.09832	-85.70263
smallii	hexaploid	2a-i	+	Green	M	37.17769	-85.52903
smallii	hexaploid	2b-ii	+	Green	M	37.19907	-85.54435
smallii	hexaploid	4b-i	+	Marion	K	37.47062	-85.29901
smallii	hexaploid	5a-ii	+	Boyle	B	37.63821	-84.95070
biltmoreana	hexaploid	1a-ii		Metcalfe	M	37.09838	-85.70234
biltmoreana	hexaploid	2a-ii	+	Green	M	37.17739	-85.52907
biltmoreana	hexaploid	2b-i	+	Green	M	37.19743	-85.54287
biltmoreana	hexaploid	5a-i	+	Boyle	B	37.63811	-84.95082
biltmoreana	hexaploid	7b-i		Jessamine	B	37.86761	-84.69174

surface at the other extreme. Figure 2 reverses the algorithm-generated order for the second axis in order to align the diagram with ecological concepts developed elsewhere (Campbell 2011). It also compresses the scale of the second axis relative to the first, in order to provide a more convenient visual display on the page; no information is lost.

The first axis clearly segregates *Fraxinus profunda* (to right) from *F. pennsylvanica* (to left), as well as collections of *F. americana* and *F. biltmoreana* with larger leaves and fruits (to right). The second axis emphasizes segregation of *F. americana* and *F. biltmoreana* (above) from *F. pennsylvanica* and *F. profunda* (below). However, variants within *F. pennsylvanica* have little or no segregation; a more focused analysis restricted to this species is presented below. Moreover, there is only weak segregation of more pubescent plants within *F. biltmoreana* from the relatively glabrous plants here named var. *subcoriacea*. The latter are concentrated in a zone along the second axis between (above) more pubescent plants (*F. biltmoreana* sensu stricto), with much overlap, and (below) *F. americana*, with almost no overlap.

The separation of Pennsylvanica and Americana groups is imperfect, and exceptional collections deserve closer inspection. In the upper right section of Figure 2, there is an outlying collection of *Fraxinus pennsylvanica* (as var. *pennsylvanica*) surrounded by *F. americana*: *Norton 323a* from Kansas. With current taxonomic concepts, its identification is appropriate but the collection has unusually large leaves with long petiolules. Moreover, a few other collections of *pennsylvanica* have relatively large leaves and long petiolules, leading to positions in the upper right half of the diagram (above the dashed line); these are from Kansas, Tennessee, Alabama and perhaps Mississippi (*Bryson 7447* at MISS but without samaras). Further sampling and deeper analysis is needed to determine if such collections represent a distinct segregate or perhaps originate from hybridization. In the lower left half of the diagram dominated by *F. pennsylvanica*, there are several collections of *F. biltmoreana* (including var. *subcoriacea*). These have relatively small leaves, narrow leaflets or short petiolules compared to most *F. biltmoreana*. However, they all have distinctive white waxy papillose lower leaf surfaces and there is no reason to doubt identifications. The third axis provided no further useful separation of Pennsylvanica and Americana groups.

Within *Fraxinus americana* (sensu stricto), there is a wide spread of collections from left to right in the upper half of Figure 2, and some indication of two distinct clusters (upper central and upper right). Further sampling would allow a more definitive analysis, but this clustering does appear to be driven largely by the frequency distribution of samara sizes, which displays a degree of bimodality (Campbell 2017). The outlying collection at upper left is *Small s.n.* (8 Aug 1892) from Virginia which has extremely small samaras ca. 14×2.5 mm; such plants have been named var. *microcarpa* Gray. In contrast, the outlying collection at upper right (*Smith et al. 3895* from Kentucky) has unusually large terminal leaflets (10–15 cm long), not larger samaras.

Within the Pennsylvanica group, there is general separation of *Fraxinus profunda* from *F. pennsylvanica* but some outliers deserve comment. Two collections with uncertain identification, lying between typical collections of these two taxa, have been reexamined and assigned to *F. profunda* with more confidence but they appear transitional to *F. pennsylvanica*. Both of these collections are from the northeastern range-margins of *F. profunda*: *Rose et al. 8469* from Pennsylvania (with unusually sparse pubescence); and *Long 6056* from New Jersey (with unusually short samaras). Another transitional collection (*Ruth 459* from Tennessee) is retained within *F. pennsylvanica* due to its short petiolules and largely glabrous leaves, but its fruits are exceptionally large and somewhat *profunda*-like (50×5.5 mm). A more convincing collection from east Tennessee (*Kearney 832*) is provisionally identified as *F. profunda*, although it has somewhat serrate leaflet margins. Thus, even when fruits are present distinction of *F. profunda* can be somewhat subjective in such cases, especially if collections are poor.

In the analysis restricted to *F. pennsylvanica*, the first axis generally separates the southeastern variants from northwestern variants (Figure 3a). However, there is still a zone of overlap at the center, along about 20% of the whole sampled axis, especially among more pubescent plants (lower in the diagram). Outliers at the upper and lower right have already been noted in the analysis of all combined collections above (*Norton 323a* and *Long 6056*, respectively). As in the combined analysis, the second axis tends to segregate plants with larger samaras and more pubescence (Table 3). The provisional taxonomic separation of more pubescent plants is partly supported with this axis. But there is a broad zone of overlap concentrated along about 40% of the whole sampled axis, and a few collections are greatly misplaced, including some of the anomalous collections noted above.

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Table 2a. Morphometric characters used in the analysis. *Note that WHI is the only character with diagnostic value by itself for distinguishing the Americana versus Pennsylvanica groups.

CHARACTERS	DESCRIPTION
EMA	Samara emarginate: 0.5 = slight notch (< 1 mm); 1 = clear notch (ca. 1 mm)
FRP	Samara length × width
FRR	Samara length / width
FRW	Samara width in mm
FRL	Samara length in mm
WHI*	Whitish waxy papillose reticulum on lower leaf surface: 0 = absent; 1 = present
SER	Leaflet serration: 0 = < 0.25 mm deep; 0.5 = up to 0.5 mm; 1 = up to 0.75+ mm
LLP	Terminal leaflet blade length × width
LLR	Terminal leaflet blade length / width
LLW	Terminal leaflet blade width in cm
LLL	Terminal leaflet blade length (down to proximal inflexion of blade) in cm
LEF	Total leaf length in cm
PLL	Petiolule length of distal lateral leaflets (up to proximal inflexion of blade) in mm
PET	Petiole base distinctly notched around most of bud: 0 = absent; 1 = present
PUB	Pubescence dense on rachis and stem: 0 = absent or sparse; 1 = present

Table 2b. Loadings and weightings of characters in the PCA for all collections. Loadings are correlations of scores with the axis; weightings are coefficients in the linear relationship.

Variables	First Axis Loading	First Axis Weighting	Variables	Second Axis Loading	Second Axis Weighting
LLP	0.913	0.226	PET	− 0.695	− 0.225
LLW	0.881	0.228	WHI	− 0.574	− 0.202
LLL	0.769	0.179	SER	− 0.144	− 0.024
LEF	0.748	0.185	PLL	− 0.125	− 0.087
PLL	0.735	0.197	FRR	− 0.040	− 0.012
FRP	0.399	0.049	LLW	− 0.022	− 0.065
WHI	0.397	0.140	LEF	0.109	− 0.016
FRL	0.368	0.045	LLP	0.132	− 0.020
FRW	0.347	0.042	LLL	0.278	0.034
EMA	0.242	0.031	LLR	0.339	0.120
PET	0.187	0.094	EMA	0.478	0.130
PUB	0.019	− 0.037	PUB	0.640	0.195
FRR	− 0.008	0.001	FRW	0.719	0.197
LLR	− 0.242	− 0.085	FRL	0.747	0.204
SER	− 0.302	− 0.068	FRP	0.819	0.224

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Figure 2 [next page]. Principal components analysis of morphometric data from 160 collections at US. See text for outline of taxa. See Tables 1 and 2 for list of characters, loadings and weights in the analysis. First axis is horizontal; second is vertical. Tick marks are units of 0.5 in the analysis. Dashed line maximizes separation of white ashes (solid) versus greens (open/crosses): 5 greens are mixed with whites, 12 whites with greens. Listed-and-marked collections are noted in the text.

AXIS ONE: + 3.0

AXIS TWO: − 3.5

AXIS TWO: + 2.5

AXIS ONE: − 3.0

Legend (upper):
- ◇ pen. var. campestris
- △ pen. var. subintegerrima
- × profunda
- ■ biltm. var. subcoriacea
- ☐ pen. var. austinii
- ○ Open. var. pennsylvanica
- ◆ americana sensu stricto
- ▲ biltmoreana var. biltm.

Legend (lower):
- A Rose 8469 PA
- B Long 6056 NJ
- C Kearney 832 TN
- D Ruth 459 TN
- E Norton 323a KS
- F Small s.n. VA
- G Smith 3895 KY
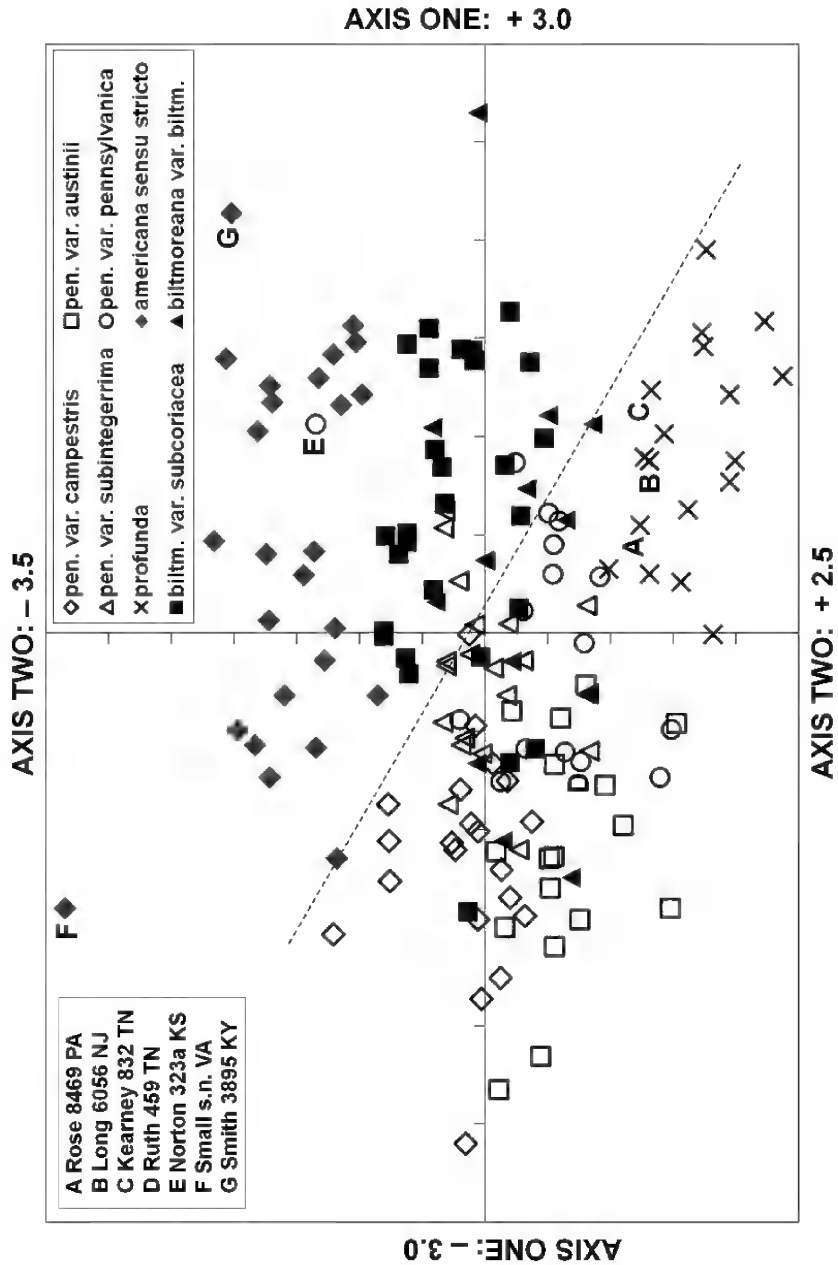
Table 3. Ranked loadings of characters (plus weightings) in the PCA for *F. pennsylvanica*. Loadings are correlations of scores with the axis; weightings are coefficients in the linear relationship. PET and WHI are excluded since those characters are uniform in this species.

Variables	First Axis Loading	First Axis Weighting	Variables	Second Axis Loading	Second Axis Weighting
LLP	0.920	0.195	FRR	− 0.392	− 0.178
LLL	0.856	0.182	PLL	− 0.162	− 0.078
LLW	0.774	0.164	LLW	0.107	0.037
LEF	0.730	0.156	SER	0.141	0.066
PLL	0.619	0.128	LLR	0.171	0.073
FRR	0.544	0.110	LLP	0.202	0.076
FRL	0.398	0.089	LEF	0.248	0.099
LLR	0.122	0.027	LLL	0.254	0.100
PUB	0.006	0.006	PUB	0.432	0.188
FRP	0.050	0.020	EMA	0.472	0.206
EMA	0.001	0.005	FRL	0.531	0.226
FRW	− 0.270	− 0.047	FRW	0.908	0.399
SER	− 0.374	− 0.077	FRP	0.921	0.401

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Figure 3a [next page upper]. PCA restricted to 74 collections of *Fraxinus pennsylvanica* scored at US. See text for outline of the four groups overlaid here, and for notes on outliers. Collections marked B, D and E are identified in Figure 2; B was reassigned to *F. profunda* after this analysis. Dashed line maximizes separation of SE variants (vars. *subintegerrima* and *pennsylvanica*) versus NW (vars. *campestris* and *austinii*): 5 NW plants mix in with the SE group; 7 SE plants mix in with the NW.

Figure 3b [next page lower]. As in Figure 3a but with geographic region overlaid instead of suggested taxa. See Figure 1 for definition of each region and further details. Dashed line maximizes separation of collections from S or E regions versus N or W: 16 N/W plants mix in with the S/E group, 5 S/E plants mix in with the N/W group.
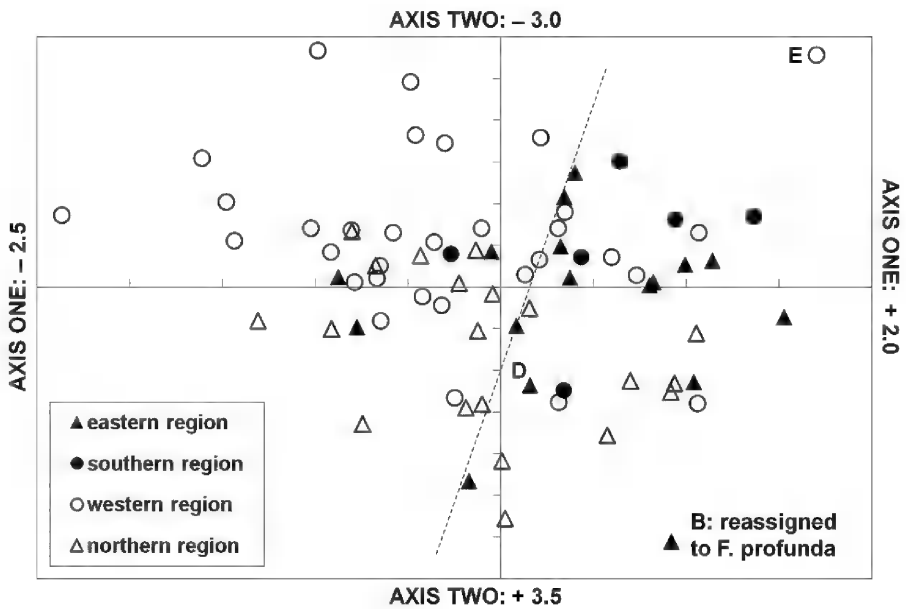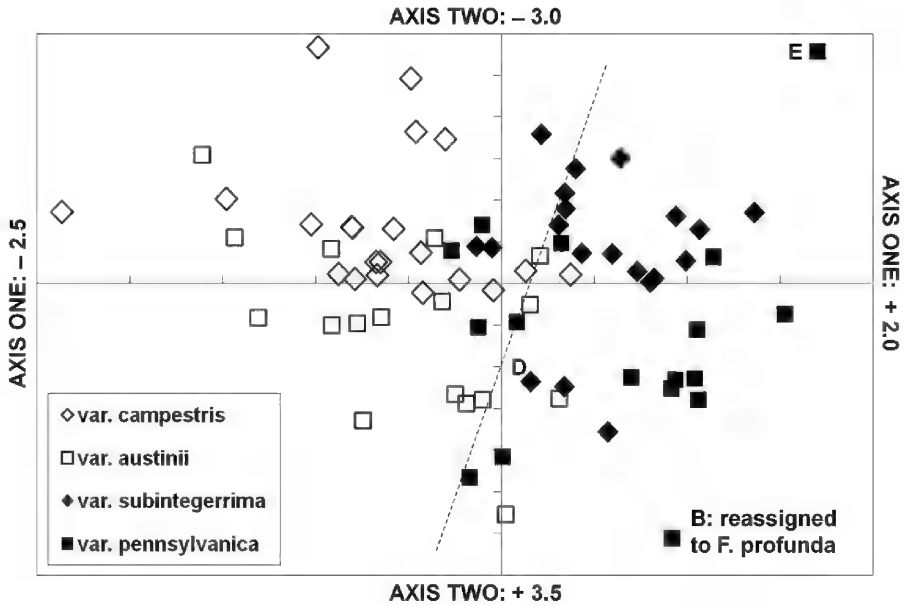
DISCUSSION
Distinction of Americana group versus Pennsylvanica group

Nesom's (2010a-f, 2014) work has supported a relatively divisive treatment of sect. *Melioides*, leading to about 15 species in North America, mostly assigned to the Americana group and the Pennsylvanica group. However, he noted potential difficulties in initial phylogenetic analysis due to uncertain identifications, and due to possible hybrid origin of some taxa. Distinction of the two major groups can be challenging among collections without samaras; about 1-10% of such collections remained uncertain in assignment after initial inspection by this author. The most useful key characters that separate the two groups include color and texture of lower leaflet surfaces (with waxy papillae and ridges in Americana group), decurrence of samara wings below seed summits (less so in Americana group), and elongated shape of seed-containing bodies (less so in Americana group). As detailed above (in notes before keys), several additional characters have been suggested by other authors, at least with reference to *Fraxinus pennsylvanica* versus *F. americana* (e.g., Miller 1955, Taylor 1972). Taylor reported that even if leaflet waxiness and petiole-notching are omitted from analysis, consistent multivariate discrimination of these two species is possible based on other characters. And in the field, habitat is often a useful guide to identification, or perhaps a bias—the Americana group generally occurs on drier ground, except perhaps for *F. pauciflora* (Tables 5 and 6).

As reviewed in the Introduction, there is little published evidence of natural hybridization between these two groups. After examination of over 2000 herbarium collections for this study, less than 20 were noted as possible hybrids. These puzzling collections mostly lack fruits, and definitive identification has not yet been possible; the few with samaras need to be studied further (e.g., from Calumet Co., Wisconsin, and Coos Co., New Hampshire, at MU). It can be sometimes be difficult to classify non-fruiting collections based on petiole bases, bud scars, or the presence versus absence of whitish waxy-papillose covering on lower leaflet surfaces (especially leaves from seedlings or shade). Some extra waxy covering can still rarely appear in *Fraxinus pennsylvanica*, as in a fruiting collection from North Dakota (*Lunell*, 16 Jul 1905 at NA), but without the papillose condition of *F. americana*.

The existence of *Fraxinus pauciflora* as a distinct species in the Americana group has been recently confirmed (Nesom 2010d), and estimates of its chromosome number are underway (A. Whittemore, pers. comm.). But provisional identifications for some collections of *pauciflora*-like plants have suggested to Miller (1955) and this author that there may be an intergrading complex between *F. caroliniana* (a highly variable taxon) and other species. There is a need for deeper investigation of such collections at US, NCU, VPI, GA, FLAS and elsewhere, including those named by Fernald (1937, 1938) as *F. caroliniana* var. *pubescens* (*Fernald 15140* from Virginia at NY) or *F. pennsylvanica* var. *austinii* (*Fernald & Long 11110* from Virginia at VPI); a possible *caroliniana-pennsylvanica* hybrid (*Fox 1738* from North Carolina at FLAS); and a possible *caroliniana-profunda* hybrid (*Price,* 9 May 1949, from North Carolina at NA).

Although several authors, as reviewed by Nesom (2014), have hypothesized that supposed polyploids in some eastern species of *Fraxinus* (*profunda, smallii, biltmoreana*) originated from hybrids, these taxa display no characters to indicate that crosses between two existing parental species are more likely than autopolyploidy from a more homogeneous ancestral pool. In *F. biltmoreana* (including *F. smallii*), the lack of notches in petiole bases has suggested hybrid origin from an *americana*-like ancestor with notches and a *pennsylvanica*-like ancestor without notches. But since petiole-notching is unique to *F. americana* (sensu stricto) within sect. *Melioides*, this character is probably derived from an un-notched ancestral pool within the Americana group. Moreover, those ancestors were presumably closer to the Pennsylvanica group than their modern derivatives. Such closeness would accord with other claimed similarities to the Pennsylvanica group in some collections of *F. biltmoreana*, including "lateral buds rounded, usually reniform" (Miller 1955), paler

brown versus darker to blackish buds in general (Yatskievytch 2013), samaras with "bodies that tend to be dark orange at maturity" (Nesom 2010f), and flavonoid profiles (Black-Schaefer & Beckmann 1989). Yet these characters are not clear or consistent enough to be diagnostic. Flavonoids may be useful but much more sampling is needed; an earlier study provided different results (Fitzgerald & Reines 1969).

Extent of polyploidy and status of associated segregates

Within the Pennsylvanica group, almost all reported chromosome counts are 2n = 46 (Saxe and Abbe 1932; Taylor 1945; Wright 1957; S. Taylor 1972; Mukherjee & Ware 1979; Löve & Löve 1982; Hickman 1993; Nesom 2010c-d). The only report of a tetraploid (2n = 92) is for *Fraxinus coriacea* (Taylor 1945). The only report of a hexaploid (2n = 138) is for *F. profunda* (Wright 1957). These sparse data do not provide strong support for a general polyploid condition in any taxon, but it is often assumed that *F. profunda* is hexaploid and derived from diploid *F. pennsylvanica* through autopolyploidy, or from a cross with tetraploid *F. americana* (Miller 1955; Wright 1965). More reliable counts are clearly needed. Within the Americana group, there are more reports of polyploidy, but there is again much uncertainty in the geographic extent and degree of correlation with morphology. And although there have been several independent reports of diploid status (2n = 46) for *F. americana*, even these are mostly from old or obscure literature without cited collections (Sax & Abbe 1932; H. Taylor 1945; S. Taylor 1972; Mukherjee & Ware 1979; Weng & Zhang 1992); only the latter two references are provided for the *F. americana* complex in the Index to Plant Chromosome Numbers (Goldblatt & Johnson 2015).

Virtually no cited collections have been clearly associated with estimations of tetraploid or hexaploid status. The only verifiable report may be Santamour's (1962) linkage of hexaploid status with "*biltmoreana*" morphology in the following collections: "One specimen each of two lots (Nos. 152 from Owen County, Indiana, and 471 from Marshall County, West Virginia)." And even in this case it is not known if collections were provided to a public herbarium. Taylor (1945) had reported 2n = 46 for "*F. biltmoreana*" from "SCS Nurs., Shiprock, N. Mex., col. Farmington, N. Mex.," with accession number 2147-39 at the Blandy Experimental Farm, University of Virginia. But Miller (1955) reported that an immature collection of this same tree at BH (Bailey Hortorium) was definitely not *Fraxinus biltmoreana* and probably in the *F. pennsylvanica* complex.

Tetraploids of *Fraxinus americana* sensu lato were not indicated in this study using flow-cytometry with material from central Kentucky (Table 1), which included plants referable to *F. smallii* in the sense of Nesom (2010f). Moreover, C. Carlson, R. Olsen, and A. Whittemore (National Arboretum, pers. comm.) have been unable to find tetraploids in mid-Atlantic states using flow-cytometry, even with several plants that have the morphology of Nesom's *F. smallii*. There are two general explanations for this discordance with the research summarized by Nesom (2010f): either (1) recent flow-cytometry at the National Arboretum is flawed as an indicator of ploidy, although direct counts of chromosomes have been made in a few cases for verification (A. Whittemore, pers. comm.); or (2) some of the earlier cytological results are unreliable and led to an overestimated range for tetraploids.

It is unlikely that recent usage of flow-cytometry at the National Arboretum has provided erroneous indications of ploidy in *Fraxinus*, but further checking and refinement of methods may be needed. R. Olsen and A. Whittemore (pers. comm.) will address these issues in a broader report of data from across the range of *F. americana* sensu lato. It is notable that their laboratory has produced good evidence of diploids and tetraploids in *Ulmus americana* (Whittemore & Olsen 2011). Nevertheless, any attempt to estimate ploidy from nuclear DNA content must consider the potential challenges and biases in methods used (Bennett & Leitch 2005, Doležel & Bartoš 2005). Moreover, there is general evidence among angiosperms that DNA content does not increase in linear proportion

to ploidy, suggesting that "loss of DNA following polyploid dormation, or genome downsizing, may be a widespread phenomenon of considerable biological significance" (Leitch & Bennett 2004). And at much smaller, physiological scales, one can expect considerable variation in DNA content within one organism. For example, Zhong et al. (1995) found that DNA content of cambial cells in *F. americana* varies by ca. 10–20% through the seasons.

The second general explanation for discordance with Nesom's summary (2010f) is more likely—that earlier estimates of ploidy were partly erroneous. Wright (1944a-b, 1957) claimed to have made direct counts of chromosomes, but he provided few details of methods or results and no figures of chromosomes. He appears to have relied largely on measurements of stomatal guard-cells as an indicator of ploidy. It would be desirable to have a more robust statistical distinction of supposed diploids, tetraploids and hexaploids using stomatal data (Table 4). Nesom (2010f) also noted general concerns about the accuracy of such distinctions.

Santamour's (1962) paper also lacked sufficient detail for robust conclusions, since he appeared to rely largely on Wright's initial assessments of ploidy in the plantation at Morris Arboretum, and perhaps subsequently on guard-cells: "In the spring of 1959 root tips were collected from these trees, pre-fixed in a saturated solution of paradichloro-benzene, killed in 3:1 alcohol-acetic, and prepared for examination by standard aceto-carmine squash techniiques. However, exact chromosome counts by this technique proved to be difficult, and some stumps did not produce new roots. Therefore, it was decided to make counts on only one tree of each progeny and to rely on stomatal guard cell measurements for verification of the degree of ploidy." Curiously, Santamour provided guard-cell measurements only from supposed diploids and tetraploids, without any from supposed hexaploids (Table 4).

Schaefer and Miksche (1977) did provide convincing indication of the three ploidies, using "photometrically determined nuclear DNA content from root tip cells of germinating embryos". Morevoer, they did check chromosome numbers using direct counts, and provided one figure of stained chromosomes that appears to show examples of the three ploidies. But, curiously, they found that only a minority (3/12) of the plants estimated to be more or less hexaploid had DNA content close to expected: 9.70 ± 0.10 pg (0.4% less than expected). The remainder (9/12) had 8.11 ± 0.08 pg, which was 16% less than expected. They invoked aneuploidy, suggesting that "some loss of chromosomal material is responsible for the lower average." In addition, one "putative pentaploid or possible aneuploid" had measured DNA content of 7.08 pg. Leser (1978), in an unpublished thesis, and Clausen et al. (1981), without new cytological data, extended the work of Schafer and Miksche (1977), and deeper assessment of their work is still needed. Armstrong and Funk (1980; Armstrong 1982) made photometric determinations of DNA content in bark cells, reporting putative diploids, tetraploids, and hexaploids as well as possible triploids and pentaploids, but they made no direct counts of chromosomes.

Black and Beckmann (1983) used photometric methods to indicate diploids, tetraploids, and hexaploids "within immediate proximity of one another" in Granville Co., North Carolina; they also reported a possible pentaploid. But, again, the degree of checking with direct counts remains dubious. Black and Beckman (1983) stated [in Methods] "Because of great difficulty in working with chromosomes of this species and in order to sample a large number of individuals, cytophotometry was used both to determine ploidy and to obtain information about the variability of nuclear DNA ... [but in Results] Chromosome counts of ten leaf cell nuclei of each tree confirmed the ploidy, within a maximum interpretation error of 2% for diploids, 7% for tetraploids, and 12% for hexaploids." However, they did not provide details of methods for making the counts, and they did not explain the meaning of "maximum interpretation error".

Taylor (1972) reported an intensive effort to count chromosomes in eastern ashes but it was restricted to *Fraxinus pennsylvanica* and *F. americana* in one southern Michigan county. Her results indicated that 2n = 46 for all 112 meiotic counts and all 76 mitotic counts. But, again, she noted difficulties in several cases, noting that "Preparations which contain a high proportion of pollen mother cells in early meiosis I stages may also contain a few tapetal cells undergoing free nuclear division and having chromosomes which appear to be paired. Because of the many, apparently paired, chromosomes of these cells, they can easily be mistaken for meiotic cells by one unfamiliar with ash tree cytology, and chromosome counts indicating high ploidal levels can result" (p. 28); and "Mitotic chromosomes from root tips were much smaller and more difficult to count. Pretreatment with paradichlorobenzene did not change their appearance significantly. At 1000× magnification it was rarely possible to distinguish more than 40 or 42 chromosomes. No count exceeding 46 chromosomes was made" (p. 29).

Given these uncertainties about earlier reports of polyploids, the current results from flow-cytometry are tentatively accepted here: that *Fraxinus smallii*, as circumscribed morphologically by Nesom (2010f), is indeed largely hexaploid rather than tetraploid (Table 1; and unpublished data). Unfortunately, there has not yet been enough accumulation of chromosome counts—or even estimates—to allow a definitive association of tetraploid or hexaploid status with the type collection of *F. smallii* by J.K. Small, which comes from the Piedmont of Georgia. Indeed, there are no published estimates of ploidy from the *Fraxinus americana* (sensu lato) complex anywhere in Georgia, where all three of the morphological taxa treated by Nesom are locally frequent.

This author's general impression across east-central states is that typical pubescent *Fraxinus biltmoreana* is often mixed with less pubescent plants in populations, especially among seedlings and saplings. Thus, it is proposed here that these less pubescent plants can be grouped with *F. smallii* as a less pubescent variant of hexaploid *F. biltmoreana*. Lack of pubescence on stems and rachises remains the only consistent character used to distinguish *F. smallii* from *F. biltmoreana*. Although Nesom (2010f) also used samara size in his key, the data from over 50 fruiting collections examined so far by this author show no significant difference in dimensions (Campbell 2017). And there are no significant differences in foliar dimensions among data analyzed above (Figure 2).

It is notable that in the most definitive cytological study of *Fraxinus americana* and allies so far, by Schafer and Miksche (1977), tetraploids were reported only from southeastern Texas (3 of 3 from that state), southern Louisiana (3 of 3) and central Mississippi (1 of 6). However, Clausen et al. (1981) reported that samaras from these same trees were similar in size to diploids and smaller than hexaploids, unlike the plants defined as *F. smallii* by Nesom (2010f). Moreover, they found that seedlings from these trees had much faster growth rates and longer growing seasons than seedlings of *F. americana* sensu lato from elsewhere across its range, when planted together in southern regions—but much lower growth and survival in northern plantations (especially Wisconsin). Thus, it remains likely that a distinct tetraploid variant does exist on the Gulf Coastal Plain. There is also some evidence that tetraploids exist on or near the Piedmont from central Georgia to central North Carolina (Black & Beckmann 1983; unpublished data of J. Campbell and A. Whittemore). It will be important to investigate the status of such plants in more detail, including consideration of the potential for "genome downsizing" (Leitch and Bennett 2004).

Table 4. Reported mean stomatal guard-cell length in *Fraxinus* sect. *Melioides*. Standard errors are based on substantial samples (see sources for details), but: "In the red ash especially it is usual to find a variation of 50 per cent in guard cell length within the same microscope field."*

Species epithet	Length (microns)	Sources
"*americana*"	15-30 [in his key]	Wright 1944b
	12-18	Taylor 1972
2x (14 progenies)	18.8±0.2	Wright 1944b
2x (11 parents)	18.2±0.3	Wright 1944b
2x (8 progenies)	16.8±1.1	Santamour 1962
4x (2 progenies)	21.6±0.3	Wright 1944b
4x (2 parents)	22.5±1.1	Wright 1944b
4x (9 progenies)	22.6±0.9	Santamour 1962
6x (4 progenies)	24.2±0.6	Wright 1944b
6x (4 parents)	23.7±0.4	Wright 1944b
"*biltmoreana*"	15-30 [in his key]	Wright 1944b
pennsylvanica	15-24	Wright 1944b*; Miller 1955
	16-28	Taylor 1972
profunda (*tomentosa*)	22-34	Wright 1944b; Miller 1955

Table 5 [next page]. Some typical characteristics of taxa in the Pennsylvanica group, based on the literature (Miller 1955, Correll and Johnson 1970, Clausen et al. 1981, Burns and Honkala 1990, Hickman 1993, Nesom 2010a-f, etc.) plus direct study of herbarium collections (especially *campestris, pennsylvanica, profunda*).

See Nesom (2010a-f) for full names with authors. The names of taxa are provisional in some cases; those with asterisks (*) are treated in this paper as weakly segregated varieties of *Fraxinus pennsylvanica: campestris, austinii, subintegerrima* and *pennsylvanica*. Note that: *velutina* should include *papillosa* according to Nesom (2010f); *profunda* includes *tomentosa* and *michauxii; caroliniana* has often been defined to include *cubensis* and *pauciflora* (Nesom 2010d, Ward 2011).

Shading indicates higher character values.

Under "Pubescence": S/s = stem; R/r = rachis; B/b = blade lower surface. Upper case indicates wide extent; lower case indicates limited or variable extent; parentheses indicate largely restricted to veins.

Under "Leaflet Width": S/s indicates taxa with more distinct margin serration; upper case indicates especially distinct.

Table 5 [see previous page for caption].

CHARACTERS	coriacea	velutina	berlandieriana	campestris* + austinii*	pennsyl.* + subint.*	profunda	caroliniana	cubensis
Range	SW desert	SW canyons	ne Mex. Tex. Okl.	c-ne US Canada	e US	e-se US	se US coast	s Fla. Cuba
Habitat:	riparian	riparian	subhydric	subhydric	subhydric	hydric	hydric	hydric
Max Height: m	5-10	9-14	10-18	12-18	15-35	15-40	3-15	3-14
Pubescence: stem rachis blade	b	S R B	(b)	s r b	s r b	s r b	(b)	(b)
Leaf Length: cm	6-15	10-25	10-15?	15-25	20-30	20-45	12-40	12-23
Leaflets: number	3-5	3-7	3-5(7)	5-7	5-9(11)	5-9	5-9	3-7
Petiolule Length: mm	5-10(13)	0-2	2-6(12)	1-3	2-4	5-12(20)	2-3(12)	4-10
Leaflet Length: cm	3-10	2-7.5	5-10	6-12	8-14	9-15(25)	4-12	5-12
Leaflet Width: cm	2-5.5 s	1-3? s	2-4 S	2-4 s	3-5	3.5-7.5	2-3	2-5
Samara Length: mm	18-32	10-35	25-35	30-40	35-45	42-65	35-46	25-54
Samara Width: mm	4-6	3-6?	3-6?	3-8	4-6	6-11	10-23	6-10
Seed-body L; mm F = flattened	9-16?	8-15?	10-18? F	12-20	15-22	18-30 f	20-35 F	15-25 F
Seed-body Width: mm	2-4?	2-4?	2-3?	1-2?	1.5-2.5	2-4	2-3	1-2

Systematic variation among eastern taxa of the Pennsylvanica group

Table 5 summarizes visible characteristics of the eight taxa recognized here within this group. These eight taxa are largely separated by range, except that within southeastern states there is also some local segregation along the gradient of increasing wetness: *Fraxinus pennsylvanica* to *F. profunda* to *F. caroliniana*. There are general increases in leaflet size and samara size from the arid west to the humid southeast. Maximum size, leaf dimensions, and samara dimensions tend to be highest in *F. profunda*, which also has the highest reported chromosome number (Wright 1957). These taxa have all been considered species by at least one previous author, as reviewed by Nesom (2010a-f). But some authors, especially Miller (1955), have reduced them to as few as two or three species based on claimed evidence of intergradation. With little quantitative support for taxonomic concepts, uncertainty remains in some cases, such as *F. pennsylvanica* var. *campestris* (Britt.) F.C. Gates and var. *austinii* Fern. Those two taxa are separated in the key above, based largely on pubescence (which is denser in var. *austinii*). They could be reasonably combined with each other, but together they remain relatively distinct from var. *pennsylvanica* plus var. *subintegerrima*.

Fraxinus pennsylvanica **vars.** *campestris* **and** *austinii*.

Despite Small's (1933) acceptance of *Fraxinus campestris* as a species, Fernald (1950) did not mention it at all. However, Fernald appears to have included some trees that are at least transitional to it under *F. pennsylvanica* var. *austinii*, which has relatively pubescent leaves and broad short samaras: "Banks of streams, Que., to Sask. and Mont., s. to N.S., N.E., Va., O., Ill. and Ia. Passing into... Var. *subintegerrima*..." Under *pennsylvanica*, Gleason (1952) stated: "Plants with subsessile lateral leaflets; sometimes pubescent as in our first variety [var. *pennsylvanica*]; sometimes glabrous like the second [var. *subintegerrima*] occur frequently to the w. of our range [ne US and adjacent Canada] and have been observed as far e. as Mich. and Ont. They have been described as *F. campestris* Britt., but probably scarcely deserve segregation."

Meuli (1936, Meuli & Shirley 1937, Rudolf 1953) showed that more northwestern plants of *Fraxinus pennsylvanica* in the Great Plains, matching var. *campestris*, tend to be more drought-resistant. Similar results were later reported by Abrams et al. (1990). Provenance trials led to one particular male tree of this type becaming widely propagated across North America as "Marshall's Seedless". According to Santamour and McArdle (1983) and others, this cultivar came from Utah, at or beyond the western range-margin of *F. pennsylvanica*. They cited: "Cole Nurs. Co., Painesville, Ohio, Fall 1955 Trade List, p. 7—handsome, shapely tree with extremely dark green glossy foliage, entirely free of seed. Porter-Walton Co., Salt Lake City, Utah, Garden Book No. 46 (1946), p. 56, offered male green ash propagated from 'non-seed-bearing trees.' Some of this material was purchased by Marshall Nurs., Arlington, Nebraska, who, in several undated listings offered 'Seedless Ash.' Cole Nurs. Co. purchased plants from Marshall, and were the first to use the cultivar name. Because of its origin as 'trees' in Utah, this cultivar name may actually apply to several genotypes." Cultivars from western states, especially Marshall's Seedless, have been widely planted in developed areas of eastern states within the past 50 years but tend to grow poorly in southeastern states (Santamour & McArdle 1983; Gilman & Watson 1993). A "very similar" cultivar from Alberta, Canada, is "Patmore" (U.S. Plant Patent PP04,684 in 1981); see <missouribotanicalgarden.org> for details.

We need more thorough surveys in herbaria to map distributions of these *Fraxinus* taxa. It is usually easy to distinguish typical plants of var. *campestris* such as Marshall's Seedless from southeastern variants of *F. pennsylvanica*, but identification can be difficult, especially for collections of seedlings. Seedlings and sprouts of var. *subintegerrima* often appear to have more serration on leaf blades than mature trees, leading to confusion with var. *campestris*. Pubescence is not a useful character; both northwestern and southeastern plants include relatively glabrous and pubescent variants, as detailed in the key above. Several collections do suggest transitions between var.

campestris and var. *subintegerrima* (e.g., *England 1402* from Marengo Co., Alabama, at AMAL). The cultivar "Bergeson" (US Plant Patent USPP4904 P in 1982) from Minnesota may match var. *campestris* but it appears transitional to var. *subintegerrima* in its relatively long petiolules, weaker leaflet serration, and longer growing season. An atypical collection of *F. pennsylvanica* from Virginia that has been referred to var. *austinii* appears transitional to *F. caroliniana* (*Fernald and Long 11110* at GH, VPI). A possible collection of var. *austinii* is known as far south as Madison Co., North Carolina (*Bozeman et al. 45185* at MUR, ?NCU), but it has relatively large terminal leaflets.

The apparent similarities of *Fraxinus pennsylvanica* var. *campestris* and var. *austinii* to *F. berlandieriana* and *F. velutina* deserve deeper investigation (Table 5). Var. *campestris* appears generally intermediate in overall dimensions of leaves and samaras between southeastern variants of *F. pennsylvanica* (including var. *subintegerrima*) and *F. berlandieriana* or *F. velutina*. Moreover, its leaves are more clearly serrate than those of typical *F. pennsylvanica*, a character shared with all western members of the Pennsylvanica group—*F. berlandieriana*, *F. velutina* and *F. coriacea*. Var. *campestris* may be closest to *F. velutina*, given its short petiolules, its tendency to dense pubescence (when grading into var. *austinii*), and its generally somewhat abrupt expansion of samara wings above the middle (unlike some *F. berlanderiana*, most *F. profunda* and *F. caroliniana*); see Nesom (2010c-d) for details. If such similarities prove stronger than those with southeastern variants of *F. pennsylvanica* then species status might even become considered for *campestris*.

Western extent of native range in *Fraxinus pennsylvanica*.

The western boundary of this species extends from eastern Alberta through eastern Colorado to southern Texas (Little 1971; Gucker 2005; Kartesz 2015). Kartesz has indicated that trees in western Washington, western Oregon, Idaho, Utah, Arizona and New Mexico are all adventive. No other species in sect. *Melioides* are mapped as native or adventive along the western boundary of *Fraxinus pennsylvanica*, other than slightly overlapping species further to the west and south (*latifolia, velutina, berlandieriana*). But given that "Marshall's Seedless" comes from a nursery in Utah, as noted above, is it possible that *F. pennsylvanica* var. *campestris* is native to that region? Some herbarium collections of *F. pennsylvanica* from Utah and New Mexico could be interpreted as native without further information, for example: *L.C. Higgins 10349* (NY), 27 Jul 1977, Utah, "Cache National Forest, Bear River Range, Logan Canyon about six miles east of Logan along Logan River"; and *B.F. Jacobs 10* (NPS: BAND), 30 Aug 2007, New Mexico, Sandoval, Frijoles Canyon at mouth, White Rock Canyon, 35.75313 - 106.25516. The latter is at the eastern edge of the range of *F. velutina*, and intergradation with that closely related species was indicated by Miller (1955); see also Table 5 and text above. However, Nesom (2010c) did not recognize any intergradation or overlapping range in New Mexico.

Under "green ash" Kuhns (2015) stated: "A tough, durable, large tree used extensively in Utah in landscapes since pioneer times. Also good for windbreaks. Lilac borers can be an especially severe problem that is difficult to treat effectively, though they may be most likely to affect stressed trees. I have seen many old green ashes that show no signs of borers, while a nearby young, vigorous, 30' tall tree might be riddled with borers. Seedless cultivars are available, but they can set large amounts of seed under stressful conditions." Yet he added (M. Kuhns, pers. comm.): "I have rarely seen green ash growing in the wild, and when I have it was in situations where it was likely volunteering from seed from domestic trees [including the *Higgins 10349* location]." Native status in Utah may be unlikely, but it still cannot be ruled out.

Variation of pubescence within *Fraxinus pennsylvanica*.

Several previous authors have distinguished relatively glabrous versus pubescent plants with different varietal names, as followed here. But this highly variable character alone is a weak basis for defining these taxa. Many collections have intermediate degrees of pubescence, and occasional

densely pubescent sprouts have been found attached to much less pubescent plants referable to var. *campestris* (e.g. *J. Campbell 2016.08.06A & B* from Vermont, and *2016.08.33A & B* from Maine, both at NY). Moreover, Taylor (1972) found that among 3-year old seedlings from glabrous mothers 20–35% were largely pubescent; and among those from pubescent mothers 40-45% were largely glabrous. However, using multivariate analysis Taylor did partially discriminate more pubescent plants (mostly referable to var. *pennsylvanica*) from less pubescent (mostly var. *subintegerrima*).

Nevertheless, some formal recognition of pubescent versus glabrous variants may be useful, pending deeper analysis of *Fraxinus pennsylvanica*. Samaras do tend to be larger in more pubescent plants, especially among the northwestern variants: *austinii* versus *campestris* (Campbell 2017). The proportion of pubescent plants appears to increase from west to east, based on overall mapping (Figure 1) and local observation. For example, in New England pubescent trees (here named var. *austinii*) are much more common than glabrous (var. *campestris*), as indicated by local floras (e.g., Haines 2011; Gilman 2015) and personal observation. But largely glabrous plants predominate in the Great Plains (e.g., Gates 1938; Correll & Johnson 1970; Lesica 2012; Yatskievytch 2013).

Fraxinus profunda.

This remains a poorly understood taxon that is highly variable and, without samaras, it is often indistinguishable from *Fraxinus pennsylvanica*. Even when samaras are present, a few collections appear intermediate between these two species, with samaras that are smaller than typical *F. profunda* or that have less decurrent wings, and with leaflets that are generally smaller or less pubescent (e.g., *Long 6056* from New Jersey at US, *McAvoy 5959* and *Naczi et al. 10463* from Delaware at APSC). Some of these intermediates have been named *F. michauxii* Britt., which Britton (1908) reported "from southern New York to North Carolina, but probably has a much wider range". There are indeed similar collections from Georgia (*Duncan 23167* at MISS) and Alabama (*Hudsen 223*, and *Jackson 138* at AUA). If these intermediate collections are included within *F. profunda*, this species appears to have some multimodality of samara sizes (Campbell 2017); deeper analysis is needed.

Although typical *Fraxinus profunda* tends to have larger samaras and more decurrent wings, compared to *F. pennsylvanica*, these differences need further assessment. There is probably some overlap in size (Campbell 2017), as just noted for "*F. michauxii*". Within what is now generally accepted as *F. pennsylvanica*, trees described as *F. darlingtonii* Britt. were reported to have "long-linear" samaras about 50–75 × 4 mm (Britton 1908), but otherwise appeared close to typical *F. pennsylvanica*, which has samaras mostly 30–50 × 4-7 mm. Yet samaras longer than 50 mm may indeed be rare within *F. pennsylvanica*, including *F. darlingtonii*. At US, only one of the 74 collections of *F. pennsylvanica* had typical samara length >50 cm (51 cm in *Morton et al. 11754* from Ontario). Elsewhere, this author has seen very few collections of any eastern *Fraxinus* with samaras 60–75 mm long, as Britton (1908) reported for both *F. darlingtonii* and *F. profunda*. In *F. pennsylvanica*, the largest seen is 64 × 5 mm from Santa Rosa Co., Florida (FLAS, "var. *darlingtonii*"). Jeffrey Carstens (U.S.D.A., Ames, Iowa; pers. comm.) has measured mean lengths >50 cm in this species at only one locality (51–60 mm near Corning in sw. New York), with just 4 trees out of 210 trees sampled across the range; his maximum for an individual samara was 67 mm.

Further verification is needed for reports of samaras over 65 mm long as typical in *Fraxinus profunda*, which seem to have been repeated in several treatments (e.g., Fernald 1950; Miller 1955, Gleason & Cronquist 1991; Yatskievytch 2013). From results of this paper (Figure 4) and other studies focussed on this species (McCormack et al. 1995; Nesom 2010a; Reznicek & Voss 2012), a more accurate statement of samara size in this species (including *F. michauxii*) would be (32)42–65(74) × (5.5)6–11(12) mm, where parentheses include the outlying 1–5% of observations. The largest samaras seen so far by this author are as follows:

Shiflet, 2 Aug 1975 (VPI), Louisiana—mean 59 × 5.5 mm; maximum 65 × 6 mm;
Athey 2968 (MUR), Kentucky—mean 60 × 8.5 mm; maximum 67 × 9 mm;
Schneck, 8 May 1901 (NY), Illinois—mean 65 × 8.5 mm; maximum 72 × 10 mm;
Snyder 1262-6 (NY), New Jersey—with only two samaras, 66 × 8.5 and 74 × 9 mm.
Deam 11987 (NY), Indiana—mean 68 × 8 mm; maximum 73 × 8.5 mm;
Fox 4879 (NA), North Carolina—with few samaras but maximum of 73 × 10 mm;

Although typical *Fraxinus profunda* tends to have larger leaf dimensions (especially petiolules), compared to *F. pennsylvanica*, there is again much overlap. For example, an extraordinary fruiting collection from northern Florida clearly matches *F. pennsylvanica* var. *subintegerrima* except that its leaflets are 18–22 × 6–8 cm, within the upper range of sizes for *F. profunda* (*Godfrey 54998* at NA).

Fraxinus profunda typically has densely pubescent young twigs and lower leaf surfaces (e.g., Yatskievytch 2013), but there are several collections with relatively large *profunda*-like samaras that are partly glabrous (e.g., *Rose et al. 8469* from Pennsylvania at US; *Vincent 7501 & 7509* from Ohio at NA and MU; *Mellinger 16 Jun 1958* and *Duncan 23167* from Georgia at MISS; *Keener 3649* and *Bryson 23140* from Mississippi at AMAL; and several from Florida at FLAS). Some of these plants have been referred to *F. profunda* var. *ashei* Palmer, which was described as a largely glabrous expression of the species, distributed across its range (Palmer 1932). But Nesom (2010e) found that the type of var. *ashei* at NCU belongs with *F. pauciflora*.

Other reported characteristics of *Fraxinus profunda* include: pubescence of lower leaflets surfaces "conspicuously banded [1-5 mm wide], the edges of the bands usually irregular, the hairs longish and notably tangled" (Godfrey 1988), more scales on lower leaflet surfaces, slightly deeper notching of petiole bases and bud scars, more elongated bark ridges (Nesom 2010a, and his citations), and more swollen trunk bases, at least in deep swamps (hence "pumpkin" ash). These features deserve more quantitative investigation.

The distribution of *Fraxinus profunda* remains somewhat uncertain due to the limited numbers of clearly identified collections with mature samaras attached, due to occasional plants that appear intermediate, and due to possible plantings. Nesom (2010a) provided an updated map of county records. A few extensions are added here (Figure 1), including the largely glabrous collections noted above. Some relevant details are as follows.

Kansas. There is a convincing collection with samaras at US: *Scott Oct 1911.*

New York. Clarification of most records from the state is needed. As noted above, there are apparently native trees in Bronx Co. that have been called *F. michauxii* (Nesom 2010a). Kartesz (2015) has mapped a few other counties in southeastern New York with "adventive or introduced" status. There are also reports of possibly native trees from Tompkins Co., New York, "at the head of Cayuga Lake in Ithaca" (Miller 1955), but botanists in that state have generally considered these trees to be derived from plantings. According to R. Wesley (pers. comm.): "There are several herbarium specimens from the local area, [but] they were in people's yards or public parks and always near a road" (also http://newyork.plantatlas.usf. edu). This author recently collected vegetative material of possible *F. profunda* in Greene Co.

Tennessee. Two notable collections from eastern Tennessee at US have been referred to *F. pennsylvanica* in the past but they have relatively large samaras and leaves, appearing at least transitional to *F. profunda*: *Ruth 459* from Knox Co. and *Kearney 832* from Cocke Co. The latter may indeed be transferable to *F. profunda* (following Figure 3), although it has slightly serrate leaflet

margins. More recently, good material of *F. profunda* has been collected in Rutherford Co. of central Tennnessee by D. Estes (APSC) and J. Campbell (NY).

West Virginia. The species remains largely unverified in West Virginia. But there are some unusually large-leaved collections without samaras at WVU, initially filed under *F. pennsylvanica*, that are suggestive of *F. profunda*. And one collection from West Virginia with samaras at MUHW does appear to be *F. profunda*: *James Meadows 010*, 29 Oct 1983, "bridge at Golden Jones, 3 mi above mouth of Little Clear Cr, rich bottomland soil" [Greenbrier Co.].

Systematic variation among eastern taxa of the Americana group
Table 6 summarizes visible characteristics of the five taxa in this group, as recognized by Nesom (2014), plus two allied species that may originate from a more basal position within the phylogeny of sect. *Melioides*: *Fraxinus latifolia* and *F. papillosa* (Williams & Nesom 2010). This table also includes the Mexican species, *F. uhdei*, a semi-evergreen tree that may originate from a basal position and appears closer to the Americana group than the Pennsylvanica group. These taxa are largely separated by range or, in southeastern states, by habitat. However, their recognition in previous treatments has been inconsistent. Again, there are general increases in leaflet size and samara size from the arid west to the humid southeast, which presumably reflects ecological adaptations. Maximum size, leaf dimensions and samara dimensions tend to be highest in *smallii* and *biltmoreana*, which are the only taxa with reported polyploidy.

Distinction of *Fraxinus americana* (sensu stricto) versus *F. biltmoreana* (sensu lato).
Diagnostic differences to distinguish *Fraxinus biltmoreana* from *F. americana* remain poorly understood. Even the characteristic notched bases in petioles of *F. americana* can be difficult to assess in some cases, despite the general significance of this character (Santamour 1962). This notching often appears to be less pronounced in the middle of more vigorous shoots. Although both *F. americana* and *F. biltmoreana* appear to vary much in pubescence, the latter tends to be more pubescent on average and *F. americana* is generally considered to have glabrous leaf rachises and young twigs. Yet there are rare collections of otherwise typical *F. americana*, with fruits, that do have densely pubescent rachises and/or twigs (e.g., from sand dunes of Indiana at MU; *Chester 1609* from Montgomery Co. Tennessee at APSC; and *Olsen et al. 148* from Washington Co., Maryland at NA, a confirmed diploid). Occasional vegetative collections of this sort are known from Florida (FLAS) to New England (NY), and deserve further investigation. Although there is no current evidence of hybridization, it will be important to explore this potential process, which could lead to tetraploids (Lyrene et al 2003, Ramsey and Ramsey 2014).
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Table 6 [next page]. Some typical characteristics of taxa in the Americana group and allies (see notes in text), based on literature (Miller 1955; Correll & Johnson 1970; Clausen et al. 1981; Burns & Honkala 1990; Hickman 1993; Nesom 2010a-f; Ares 2016, etc.) plus direct study of herbarium collections, especially *Fraxinus americana* (sensu stricto), *F.* cf. *smallii* (= *F. biltmoreana* var. *subcoriacea*) and *F. biltmoreana* (sensu stricto). See Nesom (2010a-f) for full names with authors.

Shading indicates higher character values.

Under "Habitat": hx = hydroxeric; sh = subhydric; sm = submesic; sx = subxeric.

Under "Pubescence": upper case indicates wide extent; lower case, limited or variable extent; parentheses, minor extent along veins.

Note that samara and seed size may be bimodal in *F. americana*; "+" indicates that some northern populations have similar size to *F. biltmoreana* (Campbell 2017).

Table 6 [see previous page for caption].

CHARACTERS	latifolia	uhdei	papillosa	albicans	americana	smallii	biltmore.	pauciflora
Range	Wash. Ore. Cal.	central Mexico	n Mex. Ariz.	ne Mex.-Okl.	e US-Canada	se US (Gulf CP)	se US (Appal.)	Fla. Ga.
Habitat:	subhydric-submesic	submesic ?	subxeric ?	subxeric	mesic-submesic	submesic	submesic-subxeric	subhydric-submesic?
Max. Height: m	18-24	25-40	6-12	10-15	15-30	7-25?	8-35	4-15
Pubescence: stem rachis blade	s r b	s r? (b)	(b)?	(b)	r b	(r) b	S R B	(b)
Leaf Lengh: cm	12-33	15-30	8-15	13-20	20-30	20-35	20-35	15-30
Leaflets: number	5-9	7-9	5-9	5-7	5-9	7-9	7-9	3-7
Petiolule Length: mm	0-5	3-13	0-3?	5-15	3-9	3-15	3-15	5-11
Leaflet Length: cm	5-9	7-11	3-7	3-8	5.5-12	7-14	8-14	7-15!
Leaflet Width: cm	3-7	2-5	1-3	2-5	2.5-6	3-8	3-9	3.5-7
Samara Length: mm	25-50	20-40	25-30	15-26	25-38+	30-55	30-55	28-65!
Samara Width: mm	5-9	5-6	?	3-5	3-5.5+	5-8	5-8	7-12
Seed-body L: mm F = flattened	15-18	7-12	?	5-8	6-12+	8-13	8-13	16-26 F
Seed-body Width: mm	3-5?	2-3?	?	1.5-2	1.5-3	2-3.5	2-3.5	2-4

Characters of *Fraxinus biltmoreana* that are currently more difficult to assess, but which deserve further study, include leaflet color (often more deep or bluish green) and bark pattern (often with deeper or longer fissures in vertical and lateral directions); see images in Campbell (2015). In Indiana, Deam (1912, 1919) also stated that: "the leaflets of the Biltmore ash stand in a plane higher above the rachis than those of the white ash," and that leaves fall later than *F. americana*. He noted: "young trees acquiring the fissured bark character earlier than the white ash, fissures of the bark of mature trees usually deeper and the ridges correspondingly farther apart..." Deam has been almost the only botanist to publish comments on the ecology of this taxon: "In the original forest, the pioneers called the very large ash with deeply fissured bark "the old fashion" ash. It is believed that most of the trees so described were of this variety. In the hilly parts of Indiana, this variety is found in situations too dry for the species, and for this reason should be given preference in hillside planting." There are also provisional data from Kentucky and other states that indicate a concentration of *F. biltmoreana* on drier or poorer soils than typical *F. americana*, especially in Appalachian regions (Braun 1950; Campbell 2011).

Variation within *Fraxinus americana* (sensu stricto).

If the Americana Group contains just two species in east-central states—*Fraxinus americana* (sensu stricto) and *F. biltmoreana* (including *F. smallii*), there is still considerable variation in samara size, leaf pubescence, leaflet shape and other characters within each of these. However, there is no evidence to support further taxonomic segregates of *F. americana* at this time.

As detailed elsewhere, there does appears to be a bimodal tendency in the size distribution of samaras within *Fraxinus americana* (Campbell 2017), and larger samaras are locally predominant in northern regions (Miller 1955; Nesom 2010f). Also, a few collections have exceptionally small samaras, including some that have been named *F. americana* var. *microcarpa* Gray, such as the outlier in Figure 2. Collections with samaras ≤26 mm were recorded at US and NY only from south-central states (AL, GA, KY, MO, NC, SC, TN and VA). However, the increase in average size of *F. americana* samaras with latitude is gradual, based on initial analysis of collections (Campbell 2017). In contrast, there is less variation in samara size of *F. biltmoreana* (including *smallii*), a more southern species, and this has no relationship to latitude. There is much overlap in samara size between these two species, and if they are combined as traditional "white ash", the clinal relationship of samara size to latitude largely disappears (Campbell 2017).

Clausen et al. (1981) also studied variation in samaras of *Fraxinus americana* sensu lato, and showed that overall size, seed size, and percent filled seed increases from southwest to northeast. *F. albicans* (= *F. texensis*) is a closely related species, treated as a variety or subspecies by some authors, that is largely restricted to Texas (Nesom 2010b). It has generally smaller leaves, with distinctive suborbicular-obovate leaflets, and samara size only (12)15–26(35) × 3–5(6) mm. As reviewed by Nesom, intergradation with *F. americana* is not verified, but deeper genetic analysis of the overall geographic trend in samara size is clearly warranted.

Other characters probably have latitudinal trends as well. And Wright (1944a) indicated that *Fraxinus americana*, excluding *F. biltmoreana*, could be divided into northern versus southern ecotypes, based on an extensive survey. His northern plants tended to have less leaf pubescence, narrower leaflet shape, and faster seedling growth rates in Massachusetts (at Harvard Forest). However, this author could find no significant geographic trend in leaflet size or shape among herbarium collections at US.

Additional characters should be explored in more detail with larger samples. For example, it is notable that, in the sample here from US, distinctly serrate leaflets with teeth mostly 0.5–1 mm deep were recorded only in a few northern and western collections. These were from Kansas, Iowa*,

Quebec and Vermont*; see also photos from Minnesota (Campbell 2015, p. 37). In addition, some of these collections have relatively large samaras (30–41 mm long) and in two cases (*) petioles appear to lack distinctive basal notches, suggesting *F. smallii*; some have been named *F. americana* var. *juglandifolia* (Lam.) K. Koch.

Variation within *Fraxinus biltmoreana* (sensu lato).

Britton (1908) described *Fraxinus smallii* as distinct from *F. biltmoreana* in its more decurrently winged samaras, suggesting a closer similarity to *F. pennsylvanica*. However, neither Nesom (2010e) nor this author have found that *smallii*-like plants have distinctly decurrent wings. Moreover, both *smallii*-like plants and typical *F. biltmoreana* can easily be confused with *F. pennsylvanica* based just on overall dimensions of samaras and leaves (Figure 2). The inclusion of *F. smallii* within *F. biltmoreana,* under the new combination var. *subcoriacea*, is a provisional suggestion that allows continued classification of relatively glabrous versus pubescent plants. Reasons for this combination are as follows.

(a) Both taxa appear to be generally hexaploid in east-central states based on recent results (Table 1; A. Whittemore & R. Olsen, pers. comm.).

(b) Although Nesom (2010f) indicated that *F. smallii* tends to have smaller samaras, there is no significant difference in samara size among collections at US and NY (Campbell 2017), and continuing data collection from other herbaria (not shown here) has confirmed this conclusion.

(c) Among non-fruiting collections, distinction of *F. smallii* has been based largely on its less pubescent rachis and stem surfaces (Nesom 2010f). However, several collections do have an intermediate degree of pubescence—often with dense hairs on lower leaf surfaces but thinly pubescent to glabrous rachises and stems. A quantitative survey of pubescence patterns is needed to determine whether this variation is continuous or not.

(d) Within the woods of southern and western Kentucky, the author has repeatedly found a general mixing of less pubescent *smallii*-like plants with more pubescent typical *F. biltmoreana*. There appears to be little ecological segregation, although *smallii*-like plants are generally rare to absent in the Bluegrass region of north-central Kentucky. Also, they may be concentrated on more mesic sites. Again, quantitative surveys are needed.

(e) In Kentucky, the proportion of *smallii*-like plants appears to be generally higher in shade versus sun, and among seedlings or sprouts versus branches of mature trees.

(f) A tree with generally pubescent stems and rachises near Perryville in Boyle County, Kentucky, was found to have largely glabrous sprouts at its base, probably caused by roadside damage. This was collected for NA (Table 1) and illustrated elsewhere (Campbell 2015, p. 78–81). Combination of relatively glabrous and pubescent sprouts was also found in a cultivated tree at the University of Kentucky (*J. Campbell 2016.09-12* at NY).

Although *Fraxinus biltmoreana* has often been ignored by the botanical and horticultural community, there is a widely distributed cultivar that does belong to this species: "Urbanite" from a wild tree in Danville, Vermilion Co., Illinois (Wandell 1988). This plant was initially identified as *F. pennsylvanica,* but Dirr (1997), Jacobson (2003) and others have pointed out the error. Some recent collections of this cultivar have confirmed its hexaploid status (*J. Campbell 2016.09-6, 7, 10, 12, 94 & 95* at NY). A more recently introduced cultivar—"Jade Patina" or "Greenville"—is also reported to be hexaploid, with origin from the John C. Pair Horticultural Center at Kansas State University, but few details have been published (Griffin and Davis 2005; Hatch 2013).

More analysis of *Fraxinus biltmoreana* is needed for better circumscription of segregates, including *smallii*-like plants and other potential variants or cultivars. Ashe (1902) described *F. catawbiensis* as distinct from *F. biltmoreana* in its smaller calices and samaras. As more intensive analysis of biological differences continues, it will be interesting to determine the degree of genetic separation between these variants. And as more distributional data are accumulated, it will be interesting to determine the degree of difference in overall range and habitat.

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A NEW SPECIES OF *CEREUS* S. STR. (CACTACEAE) ENDEMIC TO HAITI

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ABSTRACT

A species of *Cereus* s. str. (Cactaceae) endemic to Haiti is here described and discussed. The species has long gone unnoticed by most botanists and cactologists, with a few exceptions such as Areces-Mallea. It has been misidentified as a species of *Harrisia*, *Leptocereus*, and *Pilosocereus*. As we are unaware of any clearly applicable name, here it is provided with a name, *C. haitiensis*, and a type specimen. This cactus is characterized by its shrubby habit to 4 m tall, stems 3–4.5 cm wide, 10–15 crenate ribs, flowers ca. 5–7 cm long, and smooth, obscurely ribbed, green to yellow fruits 9–11 cm long.

REZIME

Tèks sa a dekri yon espès *Cereus* s. str. (Cactaceae) ki leve ann Ayiti. Pandan yon bon tan, pi fò espesyalis nan domèn botanik ak rechèch sou plant kaktis pa t janm remake espès sa a, anwetan de twa espesyalis. Youn pami de twa espesyalis sa yo se Areces-Mallea. Yo te konfonn Cactaceae ak lòt espès: *Harrisia*, *Leptocereus*, ak *Pilosocereus*. Kòm nou pa okouran gen okenn non ki te deja etabli pou espès la, nan atik sa a n ap rele l *C. haitiensis*, epi nou mete l nan yon espès patikilye. Kaktis sa a prezante tankou yon ti pyebwa kout e l ka rive 4 mèt wotè, lajè tij li yo kapab 3–4.5 santimèt, arebò yo dantle (10–15 pwent), li gen flè 5–7 santimèt longè, epi li gen fwi ki lis, ki gen nèvi kip a fin twò parèt, ki gen koulè vè rive sou jòn epi ki mezire 9–11 santimèt longè.

RESUMEN

Se describe y discute una especie de *Cereus* s. str. (Cactaceae) endémica de Haití. La especie ha pasado desapercibida por la mayoría de los botánicos y especialistas en cactáceas, con algunas excepciones como la de Areces-Mallea. Se ha identificado erróneamente como una especie de *Harrisia*, *Leptocereus*, y *Pilosocereus*. No conocemos ningún nombre que le sea claramente aplicable, le damos el nombre *C. haitiensis*, y asignamos un especimen tipo. Este cactus se caracteriza por su hábito arbustivo de 4 m de altura, tallos de 3–4,5 cm de ancho, 10 a 15 costillas crenadas, flores ca. 5–7 cm de largo, y frutos entre verde y amarillo, 9–11 cm de longitud, lisos, y acanalados.

The Cactaceae contain ca. 1800 species (Nyffeler & Eggli 2010), all endemic to the Americas except a few taxa of *Rhipsalis* Gaertn. (Cota-Sánchez & Bomfim-Patrício 2010). Approximately 30 species of cacti are native to Hispaniola (Acevedo-Rodríguez & Strong 2012). During field work in northwestern Haiti by Brígido Peguero and Brett Jestrow, an unknown cactus encountered was

immediately realized to represent a species never formally described for Hispaniola. A description and discussion of the species are provided, which hereafter is referred to as *Cereus haitiensis*, sp. nov.

CEREUS HAITIENSIS A.R. Franck & B. Peguero, **sp. nov.** TYPE: **Haiti**. Nord-Ouest Dept., W of Môle gorge, vicinity of Môle-St-Nicolas, arid thickets, tree 10 ft. high, seeds black, fruit pendant and glabrous, 16 Feb 1929 [specific date from holotype], *E.C. Leonard & G.M. Leonard 13311* (holotype, US [Fig. 1]; isotype, NY). Figs. 1–14.

Cereus haitiensis is most easily identified by its relatively slender stems (3–4.5 cm wide) with spines overlapping those of adjacent areoles, 10–15 ribs per stem that are distinctly crenate with the areoles residing in the indentations, relatively short flowers (ca. 5–7 cm long), and large (9–11 cm long), obscurely ribbed fruits.

Shrubs, to 4 m high, the trunk scarcely evident or to 1 m high and 20 cm thick, branches numerous, mostly erect to ascending, occasionally divergent, bending, or breaking. **Stems** indeterminate, 3–4.5 cm wide distally, green. **Ribs** 10–15 per stem, 2–10 mm high, crenate with areoles placed at the indentations along the ribs, the areoles spaced every 11–17 mm. **Areoles** circular in outline, ca. 3–4 mm wide, white tomentose with up to 20 spines on distal portions of stems. **Spines** straw-colored, to 3.5 cm long distally on stems and usually overlapping spines of adjacent areoles, to 7 cm long basally on trunk. **Flower buds** (when well-developed, just prior to anthesis) bulbous, green, the basal tube to ca. 2.5 cm long and 1.5 cm wide with areoles with tufts of white trichomes subtended by deltoid-lanceolate bracts that are green basally and brownish red distally with acute to acuminate tips, the engorged flower bud apex to ca. 2 cm long by 2.5 cm wide and enclosed by greenish sepaloid bracts with brownish to pinkish margins and apices. **Flowers** ca. 4.5–5.5 cm long, the tube ca. 3 cm long by 6–8 mm wide, the scales near the base of the tube ca. 1 mm long by 0.5 mm wide, the scales just below the sepaloid tepals ca. 3 mm long by 1 mm wide, the upper tepals ca. 1.5 cm long by ca. 5 mm wide, containing ca. 75–150 stamens. **Fruits** 9–11 cm long by 3.5–6 cm wide, obscurely ca. 10-ribbed, surface smooth and without evident areoles, green to yellow, the outer rind 6–11 mm thick internally with few white conspicuous veins, pulp pellucid grayish to white with hundreds of seeds embedded. **Seeds** 1.6–2.1 mm long by 1.2–1.6 mm wide, brown when immature to black when mature.

Distribution. Endemic to Haiti.

Phenology. Areces-Mallea (2003: 333, 492) stated that during Dec–Jan over 80% of flowers produced in a year open synchronously in 2–4 days; buds and flowers have also been noted in Feb–Mar.

Ethnobotany. During the 2015 expedition to northwest Haiti, a Haitian guide said the fruit of this cactus was used to "alisarse el cabello" [straighten and untangle hair] (also mentioned by Julien of Boukan Guinguette, pers. comm.). The common name "grifin" in Haitian Creole has been used to refer to the plant locally (Julien of Boukan Guinguette, pers. comm.).

Additional Specimens Examined. HAITI. NORD-OUEST DEPT.: road Jean-Rabel to Môle-St-Nicolas, near Môle-St-Nicolas, terrace mountain, quaternary coral limestone, arid region, 3–4 m high, profusely branched, branches nearly as long as the main stem, upward bent, 14-ribbed, spines yellowish in color, fl. not seen, fruits greenish yellow, size of a duck's egg, perfectly smooth, pulp grayish, seeds black, 3 Jul 1925, *Ekman H-4446* (S [Fig. 2], US); along Môle Road, vicinity of Jean Rabel, arid thicket, tree 10 ft. high, branches numerous, flowers green, ripe fruit yellow, 3 Mar 1929, *Leonard & Leonard 13682* (NY, US [Fig. 1]); Môle-St-Nicolas, 2.5 m o más y muy ramificada, fl. seca ahora, Feb 1985, *Zanoni et al. 33542* (JBSD [Fig. 2]). OUEST DEPT.: Plaine Cul-de-Sac, Croix-des-Bouquets, Hab. Jouon, low limestone hills, not very common, 4–5 m tall, broom-shaped, many branched, branches erect, long as main trunk, 11–13 ribbed, fl. white, brownish on the outside, fruits

perfectly smooth, indistinctly c. 10-ribbed, elongated pear-shaped, olive-green, seeds nearly black in a gray-green pulp, 18 Dec 1925, *Ekman H-5377* (S, US).

Discussion

The description above of *Cereus haitiensis* is based on original observations, but Areces-Mallea (2003) provided additional and thorough descriptions for many characters. Notably, Areces-Mallea (2003: 488–491) reported spines on the trunk to 14 cm long, flowers usually 6.7–7.1 cm long by 5–6.5 cm wide when fully expanded with a 11–14-lobed stigma, and seeds ca. 1 mm long by 0.5 mm wide (Areces-Mallea 2003: 154). The flower measurements provided here are shorter and based solely on the dried specimen *Leonard & Leonard 13682*.

The flowering areoles devoid of long hairs, bulbous flower bud, and relatively smooth, cylindrical green to yellow fruit of *Cereus haitiensis* favor its inclusion in *Cereus* Mill. s. str. or *Monvillea* Britton & Rose (=*Praecereus* Buxb.). Britton & Rose (1920: 1, 3, 21) established *Monvillea* for slender-stemmed cacti with flowers persistent on the developing fruit, compared to their concept of *Cereus* s. str. as being thicker-stemmed with flowers quickly deciduous after anthesis (see Heath 1992; Kiesling 2010a, 2010b). The morphological differences between the two genera seem tenuous (see Croizat 1943: 258). A phylogeny based on the plastid *trnS-trnG* locus indicated that *Monvillea* could be included in a monophyletic *Cereus*, depending on the inclusion or exclusion of *Cipocereus* F. Ritter and *Cereus* subg. *Mirabella* (F. Ritter) N.P. Taylor (Romeiro-Brito et al. 2016: Appendix S1; Franco et al. 2017). The limited sampling and poorly supported clades in this group in Hernández-Hernández et al. (2011) also hinted at this relationship. Here we opt to include this Haitian endemic cactus within *Cereus* and consider *Monvillea* a synonym of *Cereus*, pending further taxonomic clarification in the group.

Cereus haitiensis may bear some relation with Venezuelan or Antillean species with short flowers and oblong fruits such as *C. fricii* Backeb. (=*C. russelianus* Salm-Dyck, nom. illeg., non *C. russelianus* (Hook.) Gardner ex Lem., fide Hunt et al. 2006; Britton & Rose 1920: 33), *C. repandus* (L.) Mill. (Britton & Rose 1920: 18, 223–224, including *C. grenadensis* Britton & Rose [=*C. repandus*, fide Hunt et al. 2006]; Howard 1989: 403, as *C. margaritensis* J.R. Johnst. [=*C. grenadensis*]), or *C. smithianus* (Britton & Rose) Werderm. (Britton & Rose 1920: 37). *Cereus russelianus*, though illegitimate (McNeill et al. 2012: Art. 53.1), was validly published, and is the type species of *Pilocereus* subg. *Oblongicarpi* Croizat (see Croizat 1943: 255; Areces-Mallea 2003: 491–492). Despite the overall similarities, no other species of *Cereus* have as many ribs (consistently) and such large fruits as *C. haitiensis*. Phylogenetic analyses of DNA sequences will be useful to determine the relationship of *C. haitiensis* with other species of cacti.

The Haitian endemic *Cereus haitiensis* has long been overlooked and until now had no name clearly applicable to it. Recent treatments have not reported any native species of *Cereus* s. str. or *Monvillea* for Hispaniola (e.g. Hunt et al. 2006; Acevedo-Rodríguez & Strong 2012). Barker & Dardeau (1930) did not report any such species or genera in their treatment of the cacti of Haiti. Erik L. Ekman remains the most prolific plant collector in Haiti (Ekman 1926; Howard 1952; Dubé 2008), and Werdermann (1931: 239–240) was apparently one of the first to recognize that the collections *Ekman H-4446* (Fig. 2) and *H-5377* were the same species and distinct from all other cacti on Hispaniola. Werdermann applied the name *C. repandus* (L.) Mill. to these Ekman specimens and is credited with having made the determination in Dec 1929 on the original labels. The protologue of the basionym of *C. repandus* described eight ribs and its references therein (Boerhaave 1720: 293; Linnaeus 1737: 182) gave an origin of Curaçao and curiously mentioned "lanungine flava", none of which correspond to *C. haitiensis*. Moscoso (1941, 1943: 402) followed Werdermann's treatment for *C. repandus*, the name of which must be regarded as misapplied to *C. haitiensis*. Later these same

two Ekman specimens (*H-4446* and *H-5377*) were determined as *Cereus* sp. by Hummelinck on 12 Nov 1937 and as *Harrisia* Britton sp. by M. Hjertson & N. Taylor in 2003.

Emery C. Leonard also collected extensively in Haiti around the same time as Ekman (Leonard 1925a, 1925b, 1927; Zanoni 1986). Two other collections of *Cereus haitiensis, Leonard & Leonard 13311* and *13281* (Fig. 1), were first identified on the original labels as *Cephalocereus nobilis* (Haw.) Britton & Rose and later reclassified as *Pilosocereus nobilis* (Haw.) Byles & G.D. Rowley by D.H. Nicolson and R.A. DeFilipps in Jun 1969. The basionym protologue of this name described five ribs, clearly not applicable to this Haitian endemic. Later these same two specimens were determined as cf. *Leptocereus* (A. Berger) Britton & Rose by N.P. Taylor in Oct 1992. Another collection of this species, *Zanoni et al. 33542* (Fig. 2), was determined as *Harrisia* sp. on the original label.

Three options have been considered in giving this endemic Haitian cactus a name. One option would be to validly publish the name of *Cereus fabiolae*, nom. inval. This name was introduced for this Haitian endemic in a dissertation focused on *Leptocereus*, for which this Haitian endemic was included and thoroughly analyzed (Areces-Mallea 2003: vii, 12–13, 28–29, 39–42, 49–56, 64–68, 74–75, 80–81, 86, 89–93, 99–100, 113–116, 119. 124–125, 131–132, 139–140, 150–154, 171, 174, 177–178, 180–181, 185–186, 196–197, 202–203, 205–208, 216–217, 220, 230, 235–236, 257–261, 272–276, 293, 333, 484–493). Efforts to locate the cited type specimen (*Areces 6795*) at NY or EKK (Areces-Mallea 2003: 488), or the type specimen (*Areces-Mallea & Proctor 6399*) of *Mammillaria jamaicensis* Areces at IJ and NY (Areces-Mallea 2001), have so far been unsuccessful. Other new names were also introduced in this dissertation (Areces-Mallea 2003), including several currently invalid names of *Leptocereus* and a subgenus of *Cereus* to accommodate this Haitian endemic cactus. These novel names are invalid since the dissertation contains no evidence of being effective publication (McNeill et al. 2012: Art. 30.8).

It was suggested that a Plumier illustration (Burman 1758: pl. 195, fig. 1; Hunt 1984: 43, 60; Mottram 2002: 90, 113; Fig. 15) represented this Haitian endemic cactus (Areces-Mallea 2003: vii, 484–486). If this were the case, then *Cereus serruliflorus* Haw. would be the appropriate earlier name for this taxon, since the Plumier illustration (Fig. 15) is the type of that name (Lourteig 1991). However, the numerous and relatively long scales on the flower tube and the rather short spines on the stem with eight somewhat rounded ribs of the Plumier illustration (Fig. 15) are more consistent with *Harrisia divaricata* (Lam.) Backeb, native to the Dominican Republic and Haiti. In contrast, *C. haitiensis* has few, sparse and relatively short scales on the flower tube and stems with rather long spines and 10–16 rather narrow ribs. The exserted stigma does not readily distinguish *H. divaricata* from *C. haitiensis* (see Franck 2016: Figs. 56A, 64B, 65A, 68B, 80, 83C, 85, 86, 88, 89, 99, 103, and 104). Only the narrowly triangular, serrulate inner perianth segments and the radial symmetry of stamens in the Plumier illustration (Fig. 15) appear to represent *C. haitiensis*. The stamens in *H. divaricata* are clustered in the bottom of the flower opening, although they circle along the upper portion as well. The inner perianth segments of *H. divaricata* are oblanceolate with an apiculate apex and can be denticulate on the margin. The other anomalous piece in the Plumier illustration, for which a cross-section is also provided, is like the apex of an oblong fruit of *C. haitiensis* fused to the floral tube of *H. divaricata* (Hunt 1984: 60; Mottram 2002: 113). Given that *Harrisia* has been confused with this Haitian endemic by others, it is likely that Plumier conflated two different species, the inner flower parts representing *Cereus haitiensis* and the flower tube and stem representing *H. divaricata*.

The second option would then be to apply the name of *Cereus serruliflorus* and restrict its lectotype to portions of the flower. Because the illustration appears to be a chimera of two species with parts fused into one flower (and fruit?), it is not straightforward to delineate precisely which

parts (such as the outer sepaloid whorl or the fruit-like object [Hunt 1984: 60; Mottram 2002: 113]) would represent the type and be confident in such an approach. Additionally, the protologue of *C. serruliflorus* is problematic in referencing the eight ribs of *Harrisia divaricata*. Since both the Plumier illustration and the protologue are admixtures of two species, the application of *C. serruliflorus* will always contain conflict.

The depiction of the stem in the Plumier illustration (Fig. 15) seems to clearly represent *Harrisia divaricata*. It seems best then to restrict the type of *Cereus serruliflorus* to the stem in order to be able to clearly apply the name *C. serruliflorus* to a single species, i.e. *H. divaricata*. Alternatively, the name *C. serruliflorus* could be proposed for formal rejection. In either case, this would allow for an extant herbarium specimen that is not a mixed collection of different plant species to represent the type of this Haitian endemic. The third and chosen option is to publish a new name (*C. haitiensis*) and declare an extant type specimen with rather specific provenance that exhibits important identifying features for this Haitian endemic cactus.

Since *Cereus haitiensis* Schelle (1907: 89; Britton & Rose 1923: 283) was a nomen nudum and invalidly published, originating apparently from horticulture, it does not affect the valid publication of *C. haitiensis* (see McNeill et al. 2012: Art. 53.1) as applied here to the Haitian endemic species.

Conservation Assessment. The species is only known to be extant in extreme northwestern Haiti, which is here considered to comprise the population for conservation assessment. The subpopulation in the Cul-de-Sac region (Mottram 2002: 90, 113) represented by Burman (1758: pl. 195, fig. 1) and *Ekman H-5377* (near Croix-des-Bouquets) is presumed extinct. We propose classifying *Cereus haitiensis* as endangered (EN), given our perceived extent of its occurrence as less than 5000 km^2 (B1), extant as a subpopulation at a single location (B1a), and its presumed population decline (B1b) (IUCN 2012). It is possible that a more precise survey may find the species to be confined to an area less than 100 km^2, which would favor its assessment as critically endangered. Though localized to one location, it appeared to be relatively abundant there.

Lectotypification of *Cereus serruliflorus* (= *Harrisia divaricata*). In a second-step lectotypification (McNeill et al. 2012: Art. 9.17), the lectotype of *Cereus serruliflorus* is restricted to the stem depicted in the Plumier illustration (Fig. 15). In this way, the name *C. serruliflorus* is more clearly applied and the chimeric elements are removed from the lectotype. Since the protologue seemed to have described elements of both *Harrisia divaricata* and *C. haitiensis*, any attempt to restrict the lectotype to one species will result in conflict (McNeill et al. 2012: Art. 9.19) with parts of the protologue that described the other species. As this is unavoidable, we have chosen what we feel is the best approach in obtaining a clearly applied name with an unambiguous and extant type specimen to the Haitian endemic cactus here referred to as *C. haitiensis*.

Cereus serruliflorus Haw., Philos. Mag. Ann. Chem. 7: 113. 1830. *Harrisia serruliflora* (Haw.) Lourteig, Bradea 5: 408. 1991. **LECTOTYPE** (first-step designated by Lourteig 1991; second-step designated here): **Haiti**. Cul-de-sac, Plumier illustration. Reproduced in Burman 1758, 8: tab. 195, fig. 1; in Hunt 1984, p. 60; and in Mottram 2002, p. 113. [Here only the stem is considered part of the type specimen, excluding the chimeric flower and the peculiar fruit-like objects from the type specimen]. Fig. 15.

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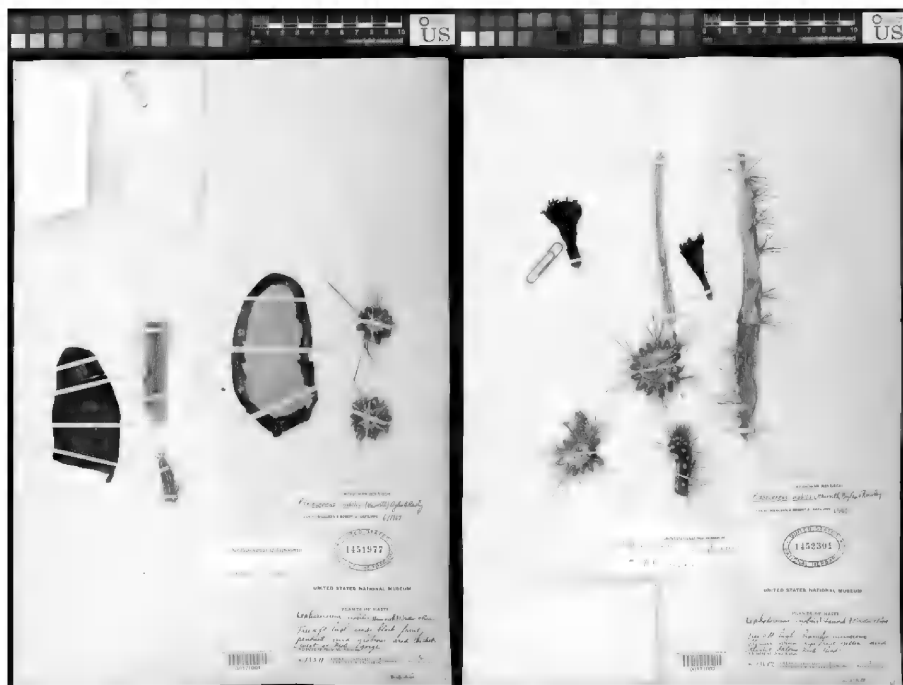
Figure 1. Specimens of *Cereus haitiensis*: *Leonard & Leonard 13311* (holotype, US) (left) and *Leonard & Leonard 13682* (US) (right). Photos courtesy of United States National Herbarium, Smithsonian Institution.

Figure 2. Specimens of *Cereus haitiensis*: *Ekman H-4446* (S) (left) and *Zanoni et al. 33542* (JBSD) (right). Photo of Ekman specimen (left) courtesy of the Swedish Museum of Natural History.

Figure 3. Habit of *Cereus haitiensis* (right foreground), at the water tank of La Batterie du Morne-à-Cabris. Photo by Barry R. Procter.

Figure 4. Habit of *Cereus haitiensis*. Photo courtesy of Boukan Guinguette - Môle / Haïti.
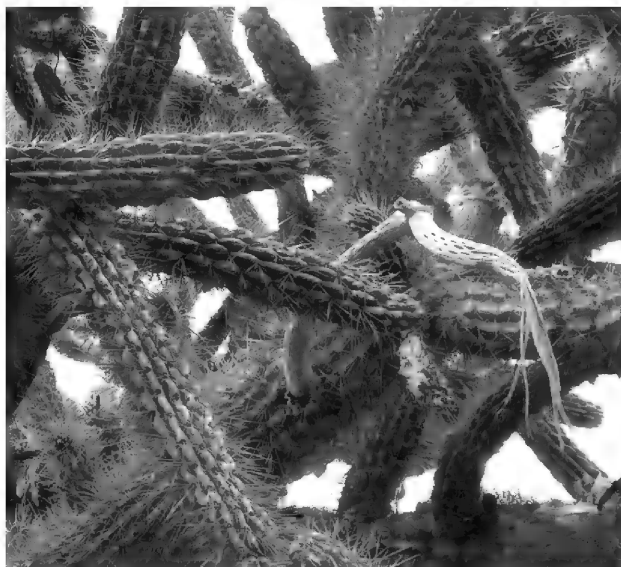
Figure 5. Crenate stems of *Cereus haitiensis*, with a dead stem showing the interwoven inner fibers. Photo courtesy of Boukan Guinguette - Môle / Haïti.

Figure 6. Crenate stems of *Cereus haitiensis*. Photo courtesy of Boukan Guinguette - Môle / Haïti.

Figure 7. Stems of *Cereus haitiensis* with bulbous flower buds, at the water tank of La Batterie du Morne-à-Cabris. Photo by Barry R. Procter.

Figure 8. Stems of *Cereus haitiensis* with one recently closed flower. Photo courtesy of Boukan Guinguette - Môle / Haïti.

Figure 9. Stems of *Cereus haitiensis* with one blackened, dried, persistent flower. Photo by Brett Jestrow.

Figure 10. Stems of *Cereus haitiensis* with one green immature fruit. Photo courtesy of Boukan Guinguette - Môle / Haïti.

Figure 11. Obscurely ribbed fruit of *Cereus haitiensis*, held by Brígido Peguero. Photo by Brett Jestrow.

Figure 12. Obscurely ribbed fruit of *Cereus haitiensis*. Photo courtesy of Boukan Guinguette - Môle / Haïti.

Figure 13. Longitudinal section of fruit of *Cereus haitiensis*, held by Brígido Peguero. Photo by Brett Jestrow.

Figure 14. Longitudinal section of fruit of *Cereus haitiensis*. Photo courtesy of Boukan Guinguette - Môle / Haïti.
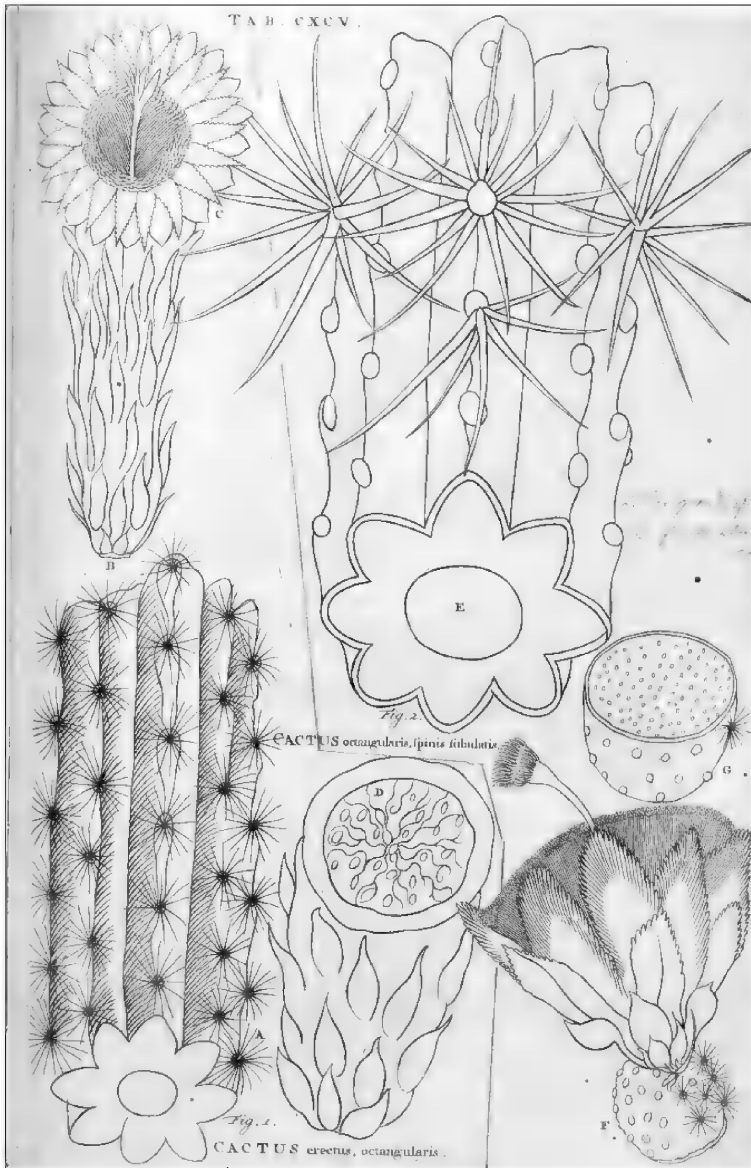
Figure 15. Plumier illustration in Burman (1758: pl. 195). The stem in the lower left corner (part of "Fig. 1" in this illustration) is designated the lectotype of *Cereus serruliflorus*. The flower in the upper left (and probably also the fruit-like object) of "Fig. 1" in the illustration is likely chimeric, with the inner perianth parts probably representing *C. haitiensis* and the tube representing *Harrisia divaricata*. Image courtesy of Peter H. Raven Library, Missouri Botanical Garden.

OBSERVATIONS ON THE PHYTOGEOGRAPHY OF THE LECYTHIDACEAE CLADE (BRAZIL NUT FAMILY)

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ABSTRACT

The Lecythidaceae clade of the order Ericales is distributed in Africa (including Madagascar), Asia in the broadest sense, and South and Central America. Distribution maps are included for the Lecythidaceae clade as follows: family maps for Napoleonaeaceae and Scytopetalaceae; subfamily maps for the Barringtonioideae, Foetidioideae, and Lecythidoideae, and maps for the subclades of Lecythidaceae subfam. Lecythidoideae. The following topics are discussed: (1) the difficulties using herbarium specimens for studies of phytogeography; (2) the worldwide distribution of the Lecythidaceae clade; (3) the migration of Lecythidaceae from the Old into the New World or *vice versa*; (4) the phytogeography of the New World subclades of Lecythidaceae; (5) the ability of some New World subclades of Lecythidaceae to occupy very large distributions; (6) the adaptations of New World Lecythidaceae to different habitats; (7) the Pleistocene refuge hypothesis; (8) the evolution of high species diversity of the family in eastern Central America/northwestern South America; (9) the possible migration of species from the Guayana lowlands and western Amazonia into Central Amazonia after large wetland areas drained after the Amazon River began to flow eastward; (10), the migration of Lecythidaceae into the Atlantic Forest of Brazil from both northeastern and southwestern Amazonia or *vice versa*; and (11) the worldwide distribution of floral symmetry of the Lecythidaceae clade.

The New World Lecythidaceae (Brazil nut family), related to members of the Old World Lecythidaceae (Figs. 1–2B), are best known for the edible seeds of the Brazil nut (*Bertholletia excelsa* Bonpl.) and the cultivation of the cannonball tree (*Couroupita guianensis* Aubl.) as an ornamental in tropical and subtropical botanical gardens. The Lecythidaceae lineage in the New World is recognized by its showy and morphologically diverse flowers with either actinomorphic or zygomorphic androecia (Figs. 3–7). In addition, the fruits are woody and dehiscent in most genera of the New World, (e.g., in the *Lecythis pisonis* clade, Figs. 8, 10J), indehiscent and berry-like (*Gustavia* clade, Fig. 8A), drupe-like (*Grias* clade), and some species are secondarily indehiscent (e.g., *Bertholletia excelsa*, Fig. 9, 10C). The spectacular flowers and fruits show adaptations for pollination and dispersal (Prance & Mori 1998) by biotic and abiotic agents. The family is ecologically dominant in lowland forests in many parts of the Amazon Basin (Steege et al. 2006) and present, but less frequent, in periodically flooded forests, cloud forests, and savannas. Species of the family, the Brazil nut tree in particular, are icons of Amazonian trees (Mori 2001). In general, if numerous species of Lecythidaceae are present in lowland forests it is likely that those forests have not been drastically disturbed by humans in the recent past (Mori et al. 2001).

This family forms a clade in the Ericales (Schöenberger et al. 2005), referred to as the Lecythidaceae clade in this paper. The combined analysis of *ndh*F and *trn*L-F genes by Mori et al. (2007) and morphological data supports recognizing Napoleonaeaceae (Prance 2004) and Scytopetalaceae (Appel 1996, 2004) as related but separate families from Lecythidaceae. Authors in Kubitzki (2004) accept the division of Lecythidaceae into the subfamilies Foetidioideae, Barringtonioideae (not Planchonioideae fide Thorne 2000), and Lecythidoideae (Prance & Mori 2004). See Map 1 for the worldwide distribution of Lecythidaceae and Table I for the current family classification and number of species in each clade.

Current phylogenies do not prohibit recognizing the three subfamilies as the families Foetidiaceae, Barringtoniaceae, and Lecythidaceae. An argument for this point of view is that there are no apparent anatomical, cytological, or morphological characters uniting them into a single family. In contrast, there are key characters that can be used to separate the three subfamilies as families (see key below). We have not made the change to recognize the three families because some characters need to be confirmed by more sampling (e.g., the orientation of the xylem and phloem in cortical bundles), and because of the lack of data for other characters (e.g., chromosome counts for *Crateranthus*, *Foetidia* and all Scytopetalaceae except *Asteranthos brasiliensis* and molecular sequences for more taxa, especially for *Crateranthus*, and *Petersianthus*). In this paper, Lecythidaceae, instead of Lecythidaceae subfam. Lecythidoideae, is used when the family is mentioned for taxa of the New World whereas the Lecythidaceae clade refers to the Napoleonaeaceae, Scytopetalaceae, and Lecythidaceae.

In a large-scale ecological study of lowland Amazonian forests (Steege et al 2006), the Lecythidaceae ranked third in total number of trees. They are surpassed in number by Fabaceae (legumes) and Sapotaceae (chicle family), but *Eschweilera coriacea* (DC.) S.A Mori. is ranked as the most abundant of all tree species in the study. In another paper, Steege et al. (2013) concluded that there are 390 billion individual trees ≥10 cm DBH and 16,000 species of trees of that size in Amazonia. The study found that 227 species (including all families) accounted for nearly half of all of the trees sampled and demonstrated how important relatively few species of Lecythidaceae and other families are for maintaining ecosystem services of Amazonian forests. Other studies have documented large numbers of individuals as well as high species diversity of Lecythidaceae, especially in central Amazonia (Mori & Lepsch-Cunha 1995) and the Guianas (Mori & Boom 1987). A 100-hectare plot inventoried by Mori et al. (2001) in central Amazonia found that 10% of the individuals and 6% of the species belonged to Lecythidaceae. In higher-elevation cloud forests, periodically flooded forests and dry habitats, New World Lecythidaceae are present but at much lower densities and species richness than in lowland non-flooded forests.
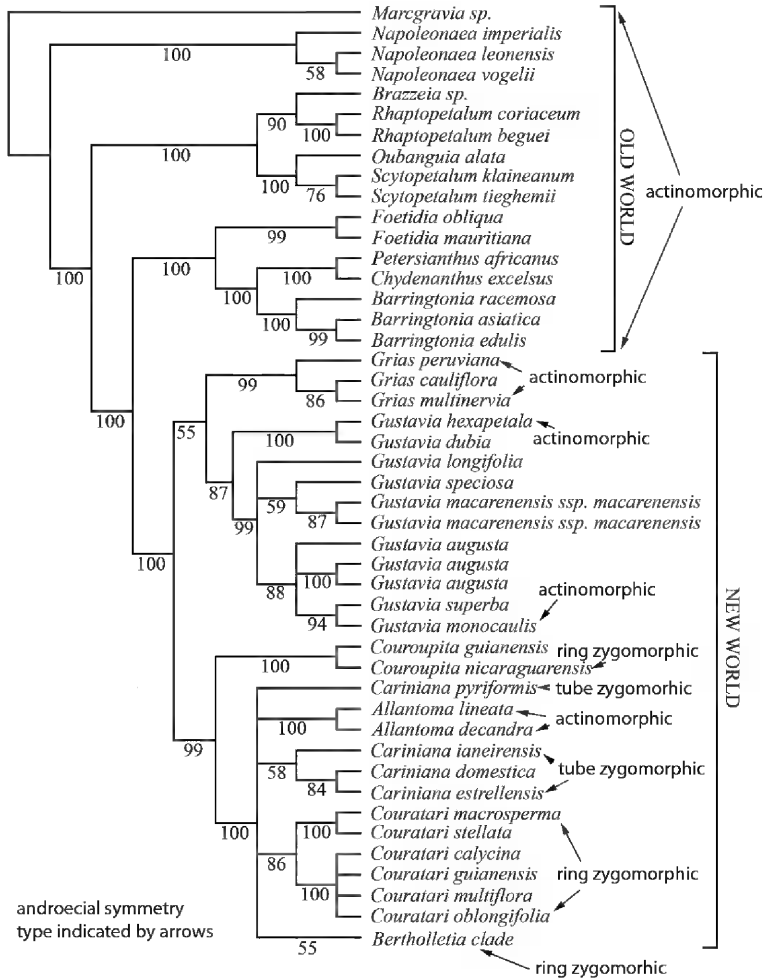
Figure 1.   The non-*Bertholletia* grade.   This cladogram includes most Old Word lineages (all with actinomorphic flowers), the actinomorphic-flowered genera of the New World, the only tubular zygomorphic-flowered genus in the clade, and two zygomorphic-flowered genera from the New World. The remaining zygomorphic-flowered genera in the New World belong to the *Bertholletia* clade (Figs. 2A–2B). The positions of the flower symmetry types are marked on the cladogram.   This is a jackknife tree generated using Xac (Farris, 1997), which is based on a combination of *ndhF* and trnL-F sequences.   From Mori et al. (2007) but modified by changing *Cariniana decandra* Ducke to *Allantoma decandra* (Huang *et al.* (2008).

Figure 2A. The *Bertholletia* clade and its outgroup as recovered by Huang et al. (2015) are represented in this and Figure 2B. Old World species of the Lecythidaceae clade are not included in this cladogram. The cladogram is based on a strict consensus of 66 most parsimonious (MP) trees based on total evidence. Boot strap values (>50%) are given above the branches. The positions of the flower symmetry types are marked on the cladogram. *Eschweilera congestiflora* and *E. simiorum* have been changed to *Lecythis congestiflora* and *L. simiorum* to reflect the transfer of these species to *Lecythis*.

Figure 2B. Continuation from 2A.
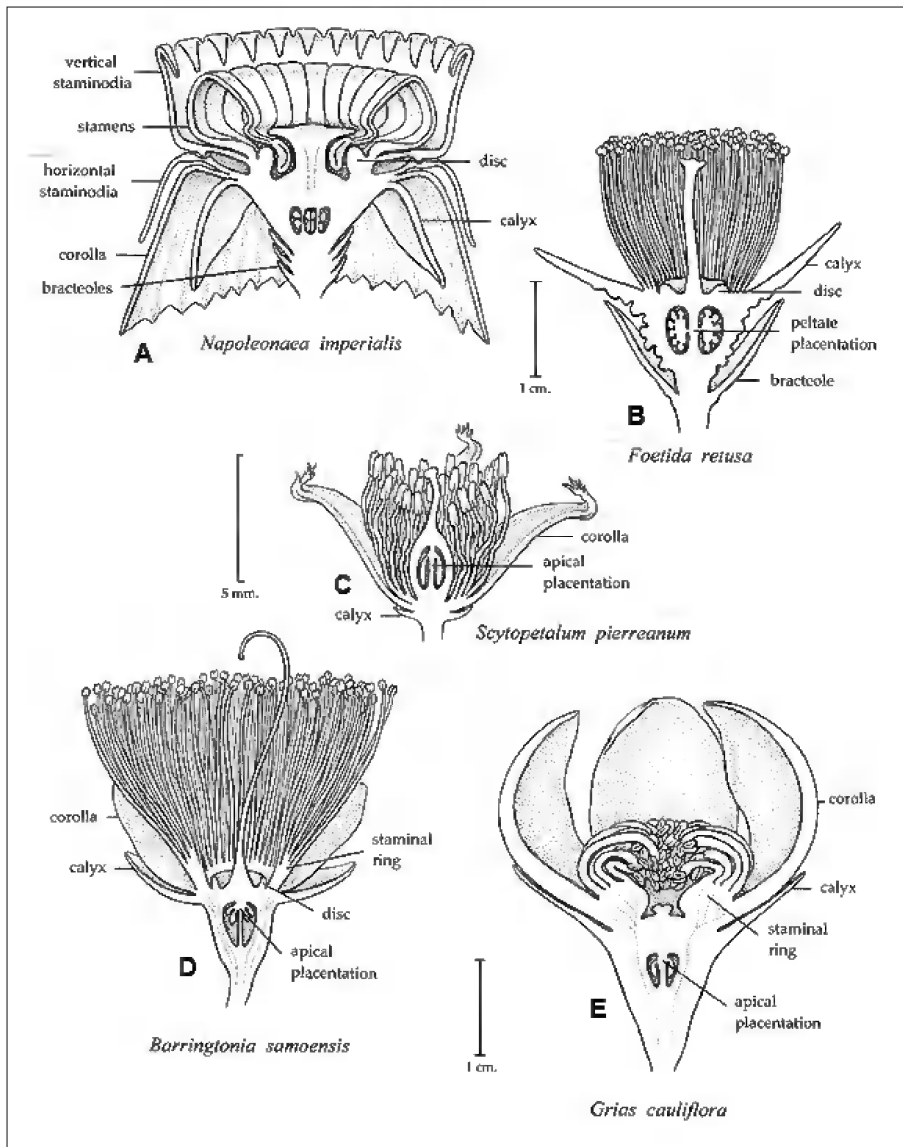
Figure 3. Flowers of the Lecythidaceae clade. A. Napoleonaeaceae. B. Foetidioideae. C. Scytopetalaceae. D. Barringtonioideae. E. Lecythidoideae. Drawings by B. Angell.

The distribution ranges of taxa of Lecythidaceae are driven by abiotic factors that isolate populations as well as create new habitats to which Lecythidaceae either adapt or become extinct. These factors include (1) formation of rivers, large lakes, or epicontinental seas and their changes over time; (2) uplift of mountains that create valleys and slopes, altitudinal differences, and different temperature regimes; and (3) soil moisture that ranges from always saturated (swamp forests), periodically saturated (along rivers), not saturated (non-flooded forests), and periodically dry areas (e.g., savannas and thorn scrub vegetation). Most species of New World Lecythidaceae grow in non-flooded forests but some have adapted to savanna, wet habitats, and cloud forests. Extreme rainfall, especially if a wet year is long and followed by consecutive wet years, can cause high mortality to species of Lecythidaceae adapted to lowland, non-flooded forests (Mori & Becker 1991). In contrast, we do not know of any species that grow in extremely dry areas such as the thorn-scrub vegetation (*caatinga*) in northeastern Brazil and the *Chacó* of Argentina or in cold areas such as the Araucaria Forests of Brazil and the *páramos* of the Andes.

In a paper about the origins of the flora of southern Brazil, Lyman Smith (1962) wrote

"Ever since the first land plants evolved, the face of the earth has been changing constantly, so that we may safely assume that the flora of any given region today has arrived from somewhere else. In the case of land recently risen out of the sea, it is relatively easy to see whence its flora came, but in the case of a great center of distribution like the Amazon Basin it is difficult if not impossible to reconstruct its past."

With the use of technologies not available to Lyman Smith, hypotheses about the geographical history of plants can now be addressed using up-to-date scientific tools. His paper represents the first step in understanding the historical biogeography of a region (eastern Brazil), whereas we present a review of the status of the phytogeography of the Lecythidaceae clade. Our goal is to make available what we have learned about this pantropical family of trees so that others can use our observations to develop and test hypotheses about the evolution and phytogeography of Lecythidaceae.

METHODS

Locality coordinates of Lecythidaceae were downloaded from The New York Botanical Garden's Virtual Herbarium and other sources, such as the Global Biological Information Facility (GBIF 2016 accessed). The data were plotted using ArcGIS 10.4 (ESRI 2017). Cultivated specimens and specimens with incorrect coordinates (e.g., plotted in the incorrect hemisphere or in the ocean), were either corrected or filtered from the group. Metadata were taken from the collections and were assigned to the data points. The data were projected to the World Cylindrical Equal Area and were merged into one layer and saved in the project geodatabase. Using the ArcGIS geoprocessing tool Grid Index Features, a grid consisting of 10,000 km^2 units was created and overlaid on the data points, joining by both one-to-one and one-to-many relationships to count all points within a grid square (join count produced in one-to-one join) and to count all distinct variables within each grid square (one-to-many join). The one-to-many join enables the counting of distinct species per grid square by exporting the information from ArcGIS to an Excel spreadsheet and using the Pivot Tables tool in Excel to expedite the counting of distinct variables. Collection density and species richness are visualized using the spatially joined collection point data to grid square, based on distinct grid ID number (auto-populated by ArcGIS).

The families Napoleonaeaceae and Scytopetalaceae and the subfamilies Barringtonioideae, Foetidioideae, and Lecythidoideae are mapped to family and subfamily, respectively. In the maps of these lineages, a dot represents the presence of the family or subfamily at that locality. In contrast, the dots on the maps of the subclades of subfamily Lecythidoideae represent collections identified to species. In some maps (e.g., the maps of the *Gustavia* and the *Eschweilera parvifolia* clades) "heat maps" are used to indicate the number of species (number in grid) and number of collections (color of

grid). This type of map is used because maps of high diversity clades become crowded and are difficult to read. Maps for all species can be viewed individually on the Lecythidaceae Pages (Mori et al. 2010). The New World subclades mapped in this paper are those recognized by Huang et al. (2015) and Mori et al. (2015).

In some maps, unrelated species grouped together illustrate congruent distributions. For example, different species with overlapping ranges in eastern Central America/northwestern South America suggest that geological events in this region caused similar distributions among numerous species (Map 23).

The presence of errors in the identification of collections (Mori 1998) and errors in mapping specimens make it difficult for botanists to accept or reject hypotheses based on data from some herbarium specimens (Steege et al. 2016). For example, Meyer et al. (2016) removed 53% of the 119 million collections studied because the discarded specimens lacked coordinates, the coordinates were incorrect, or the determinations were incomplete or obviously wrong. In this study, we corrected incorrect coordinates of some specimens (e.g., coordinates mapped in the sea) and did not include specimens with doubtful determinations.

There are two phylogenies referred to in this paper. Figure 1, based on Mori et al. (2007), represents the non-*Bertholletia* grade and its relationship with the *Bertholletia* clade. Thus, Figure 1 shows the relationships of Old and New World taxa and the placement of the *Bertholletia* clade. In the original publication by Mori et al. (2007) the non-*Bertholletia* grade was erroneously called a "clade" when it should have been called a "grade" because it is paraphyletic and the *Bertholletia* clade is derived from within it. The cladogram represented in Figures 2A–B includes only New World taxa (Huang et al. 2015).

Interactive Google maps are available for the New World species of Lecythidaceae on the Lecythidaceae Pages (Mori et al. 2010). These maps provide links to the data associated with the collections when the dot representing a collection is clicked.

RESULTS
The results of this project are the maps and their interpretations (Maps 1–27). The maps include families (e.g., Scytopetalaceae, Map 3), subfamilies (e.g., Lecythidaceae subfam. Lecythidoideae, Map 6), clades (e.g., *Lecythis pisonis* clade, Map 13), genera (e.g., *Gustavia,* Map 8), or species (e.g., *Allantoma*, Map 10). Descriptions and illustrations of the morphology of the clades belonging to the Lecythidaceae subfam. Lecythidoideae clade can be found in Huang et al. (2015) and Mori et al. (2015).

Key to the clades of Lecythidaceae *sensu lato*

1. Cortical bundles normally oriented (xylem inside phloem outside). Flowers with actinomorphic androecia and styles much shorter than stamens or flowers zygomorphic and styles shorter or only slightly projected beyond stamens; stigma small and not pentagonal; pollen tricolpate (Fig. 7A). Chomosome numbers x = 17. Native only to the Neotropics
.... **Lecythidaceae subfam. Lecythidoideae**
1. Cortical bundles normally or inversely oriented (xylem outside phloem inside). Flowers only with actinomorphic androecia and styles as long as or longer than the stamens, if shorter than stamens the stigma large and pentagonal; pollen tricolpate or syntricopate (Fig. 7B). Chromosome numbers x = 13, 16, 21, or unknown. All but one species (*Asteranthos brasiliensis* Desf. of the Scytopetalaceae) native to the Paleotropics.

2. Leaf blades with poorly defined secondary veins, the tertiary veins parallel to secondary veins. Calyx with 4, valvate, triangular lobes; petals absent; androecium with stamens free or nearly so. Fruits conical. Madagascar, surrounding islands, and nearby Africa
.... **Lecythidaceae subfam. Foetidioideae**
2. Leaf blades with well-defined secondary veins, the tertiary veins reticulate. Calyx with >4, valvate or imbricate, ovate lobes; petals present; androecium with stamens fused. Fruits globoid, ovoid, or fusiform.

> 3. Calyx-lobes with nectaries on margins; stamens 10, the filaments of stamens and staminodes fused at bases and apices but with slit-like openings in middle of staminal tube, markedly flattened, reflexed, the anthers positioned under stigma; stigma pentagonal ... **Napoleonaeaceae**

> 3. Calyx-lobes without nectaries on margins; stamens > 50, the filaments only fused at bases, without slit-like opening in middle of staminal tube, not markedly flattened, straight, the anthers positioned above stigma; stigma not pentagonal.

>> 4. Cortical bundles inversely oriented. Annular nectary usually present; pollen syntricolpate; ovary inferior. Seeds without conspicuous endosperm
>> .... **Lecythidaceae subfam. Barringtonioideae**
>> 4. Cortical bundles normally oriented. Annular nectary absent; pollen tricolpate; ovary superior. Seeds with ruminate endosperm .... **Scytopetalaceae**

Lecythidaceae clade (Map 1)

This map shows the distribution of Lecythidaceae *sensu lato* (all the families and subfamilies of the Lecythidaceae clade are mapped). The Lecythidaceae clade occurs in South and Central America, Africa, and Asia in the broadest sense (including Australia and the Pacific). The current numbers of known genera and species of this clade are found in Table I.

Napoleonaeaceae (BS 100%[Mori et al. 2007]; Figs.1, 3A; Map 2)

This is a monophyletic clade sister to Scytopetalaceae/Lecythidaceae.

This clade is recognized by the presence of normally oriented cortical bundles in the stem (xylem on inside); calyx lobes 5, not imbricate, with nectaries on margins; petals present (corona derived from petals, fide Ronse de Craene 2011); androecium actinomorphic, the stamens 10 (Frame & Durou 2001), filaments basally and apically fused but with window-like slits in middle, flat, the anthers laterally dehiscent, the pollen tricolpate *sensu lato* (Fig. 7A); intra staminal annular nectary absent (but nectar canal present, Frame & Durou 2001); ovary inferior, the style never as long as stamens, the anthers placed under stigma, the stigma, large, pentagonal; placentation not known; fruits drupes, seeds 1–20 per fruit (Liben 1971), endosperm absent, cotyledons 2, fleshy. x = 16 (Mangenot & Mangenot 1957, 1962), *Crateranthus* not known.

This West African family consists of *Napoleonaea* with eight species (Liben 1971) and *Crateranthos* with two species (Knuth 1939).

Based on descriptions and illustrations in Frame and Durou (2001), Knuth (1939), Prance (2004), and Prance and Jongkind (2015).

Scytopetalaceae (BS 100% [Mori et al. 2007]; Figs 1, 3C; Map 3)

This is a monophyletic clade sister to the three subfamilies of Lecythidaceae.

This clade is recognized by the following: presence of normally oriented vascular bundles in the stem (xylem inside); calyx fused, irregularly opening, not imbricate, rim-like or irregularly lobed, without nectaries; petals present (corona-like and interpreted to be derived from stamens by Appel, 1996); androecium actinomorphic, the stamens numerous 60–240 (Appel 1996), long, basally adnate to one another and to petals, a staminal tube scarcely developed, the anthers relatively long, with lateral or poricidal dehiscence, the pollen tricolpate (Fig. 7A); intra staminal annular nectary absent; ovary superior or semi-inferior, the style as long or longer than stamens, lobed (*Rhaptopetalum*) to slightly lobed at apex in other genera, the placentation variable, ovules axile, pendulous from apex of locule, arising along the length of the septum, or peltate-like; fruits globose or ovoid, elongate fusiform in *Pierrina*, indehiscent, drupes (exception is *Oubanguia* with loculicidal capsules), seeds 1 or very rarely 2–3 per fruit, endosperm present, ruminate in all genera except *Oubanguia*, the cotyledons flat, cordate or reduced in Asteranthos. x = 21 in *Asteranthos* (Kowal 1989) and unknown for other genera.

This family is restricted to West Africa, except for *Asteranthos brasiliensis*, which occurs in Amazonian Brazil and Venezuela. The family is divided into the subfamilies, Scytopetaloideae (*Asteranthos*, *Oubanguia*, and *Scytopetalum*) and Rhaptopetaloideae (*Brazzeia*, *Pierrina* and *Rhaptopetalum*).

Based on descriptions and illustrations in Appel (1996, 2004) and Prance and Jongkind (2015).

Lecythidaceae subfam. Foetidioideae (BS 99% [Mori et al. 2007]; Figs.1, 3B; Map 4).
This is a monophyletic group of a single genus sister to subfamily Barringtonioideae and these two clades together are sister to the New World Lecythidaceae.

The clade is recognized by the following: presence of inversely oriented cortical bundles of the stem (xylem outside); calyx 4-lobed, the lobes triangular, not imbricate, without nectaries; petals lacking, a corona not present; androecium actinomorphic, the stamens numerous (>200), not or only scarcely fused at base (i.e., staminal tube absent), the anthers small, with lateral dehiscence, the pollen tricolpate (Erdtman 1952); intrastaminal annular nectary absent; ovary inferior, truncate or slightly domed at apex, the style as long or longer than stamens, with 3–4 short lobes at apex, the placentation peltate, not apical, not pendulous; fruits obconical, thinly woody, indehiscent; seeds 1 per fruit, without endosperm, cotyledons not known. x = not known.

The secondary veins are obscure, depart from the midrib at about a 45° angle, run straight for most of distance to the margin, and the tertiary veins are parallel to the secondary veins. In the New World, all species of *Allantoma* and some species of *Cariniana* (*C. domestica* (Mart.) Miers and *C. micrantha* Ducke) also have this type of venation but the secondary veins of these species arch upward toward the margin.

The 17 narrowly distributed species of *Foetidia* are centered on the island of Madagascar. In addition, one species occurs in East Africa and two species occur in the Mascarene Islands (Prance 2008; Prance & Jongkind 2015).

Based on descriptions and illustrations in Knuth (1939), Prance (2008), and Prance and Jongkind (2015).

Lecythidaceae subfam. Barringtonioideae (BS 100% [Mori et al. 2007]; Figs.1, 3D, Map 5)
This is a monophyletic group sister to the Foetidioideae clade, both of which together are sister to the New World subfam. Lecythidoideae (Fig. 1).

This clade is recognized by the following: inversely oriented cortical bundles of the stem (xylem outside); calyx fused in bud (circumscissile or splitting irregularly at anthesis) or lobed from start, without nectaries on calyx; petals present, usually 4; androecium actinomorphic, the stamens numerous (>200), the filaments long, the anthers small, with lateral dehiscence, the pollen syntricolpate (Erdtman 1952; Tsou 1994); intrastaminal annular nectary present; ovary inferior, truncate at apex; style as long or longer than stamens, the stigma small, not lobed at apex, the placentation often with few ovules pendulous from summit of locule in *Barringtonia* but also along entire length of septum in *Careya*, and at base of septum in *Chydenanthus*; fruits indehiscent, narrowly fusiform to broadly fusiform in *Barringtonia* and *Chydenanthus*, globoid in *Planchonia* and *Careya*, and very narrowly fusiform with conspicuous wings in *Petersianthus*; seeds usually 1 per fruit in *Barringtonia* and *Chydenanthus*, numerous in *Careya* and one to numerous in *Planchonia*, not known for *Petersianthus*, cotyledons absent in *Barringtonia, Careya,* and *Chydenanthus*, leaf-like and plicate in *Planchonia* and not known in *Careya* and *Petersianthus*, endosperm absent or very sparse. x = 13 in *Barringtonia, Careya, Chydenanthus, Petersianthus, Planchonia* (Sobti & Singh 1961); Mehra 1972; Sakar et al. 1982; Singhal & Gill 1984; Morawetz 1986; Sarkar & Datta 1982; Kowal 1989; Prance & Kartawinata 2013) and x = 26 in *Barringtonia racemosa* (L.) Spreng. (Morawetz 1986; Sarkar 1982), *B. acutangula* (L.) Gaert. (Sarkar 1983), and *Petersianthus macrocarpus* (P. Beav.) Liben (Pl@ntUse 2017).

According to Prance (2012) the 69 species of *Barringtonia* have three areas of high species diversity: Malay Peninsula, Borneo, and New Guinea. There are four species of *Careya* native to India and Southeast Asia; two species of *Chydenanthus* native to Java and Sumatra; and two species of *Petersianthus*, one (*P. macrocarpus*) is African and the other (*P. quadrialatus* Merr.) is restricted to the Philippines. *Peteranthus* is the only native species of the Barringtonioideae found in west Africa where it is common and widespread. In addition, 14 species of *Planchonia* are native to tropical Asia and New Guinea.

Based on descriptions and illustrations in Kunth (1939), Kartawinata (1965), Prance (2010a 2010b, 2012), Prance and Kartawinata (2013), and Prance and Jongkind (2015).

According to Lindenmayer and Laurance (2016), *Petersianthus quadrialatus* is native to the the Philippines and, at 87.8 m, is one of the world's largest trees.

Lecythidaceae subfam. Lecythidoideae (BS 100% [Mori et al. 2007]; Figs. 2A–B, 4–10; Map 6)
This is a monophyletic group that is sister to the Foetidiodeae/Barringtonioideae clade and consists of all New World species except *Asteranthos brasiliensis* which is now placed in the Scytopetalaceae (Appel 1996 2004). The ten genera in this subfamily are restricted to the New World.

This clade is recognized by the following: presence of normally oriented cortical bundles of the stem (xylem inside); flowers with calyx only fused in bud (circumscissile or splitting irregularly at anthesis) in *Grias* (with the exception of *G. neuberthii* J.F. Macbr. which possesses 4 free calyx-lobes) or lobed from the start in other genera, without nectaries on calyx; petals present, 4 in *Grias*, 5 in *Allantoma*, and mostly 6 in other genera, androecium with four types of symmetry: (1) actinomorphic with a slightly carnose staminal tube bearing stamens along rim (*Gustavia*), (2) actinomorphic with markedly carnose staminal tube with stamens on rim and also on inner walls of the staminal tube (*Allantoma* and *Grias*), (3) obliquely zygomorphic with a slight prolongation on one side of a small membranous staminal tube and stamens inserted on the margin and inside of the tube, or (4) with a staminal ring (staminal tube absent) bearing fertile stamens and a ligular extension from one side of the staminal ring, the extension arches over the ovary and usually bears stamens or modified stamens (staminodes or vestigial stamens). The anthers usually open by lateral slits or by terminal pores (only in *Gustavia*), ovaries inferior (*Allantoma, Bertholletia, Cariniana,*

Corythophora, Couratari, Gustavia, Lecythis) or half-inferior (*Couroupita, Eschweilera, Grias*), placentation variable (Mori et al. 2015), stigma usually not divided (slightly divided only in *Grias*), endosperm usually absent (found only in *Grias* but sparse). $x = 17$ (Mangenot & Mangenot, 1958; Kowal et al. 1977; Gibbs & Ingram 1982; Guerra 1986; Morawetz 1986; Kowal 1989), *Couroupita guianensis* has been recorded to have both $x = 17$ (Kowal et al. 1977; Morawetz 1986) and $x = 18$ (Sarkar et al. 1982; Sarkar 1983). *Gustavia augusta* L. is reported to have $x = 36$ which gives it a base number of $x = 18$ (Sarkar 1983). In summary, with a few exceptions, species of subfam. Lecythidoideae have base chromosome numbers of $x = 17$.

The generic relationships of this clade has been reviewed by Huang et al. (2015) and Mori et al. (2015) and the authors concluded that *Eschweilera* and *Lecythis* are not monophyletic; therefore, there may be realignments of these genera based on future studies.

Based on descriptions and illustrations in Huang et al. (2015), Mori et al. (2015), Mori and Prance (1990), and Prance and Mori (1979).

<div align="center">NON-BERTHOLLETIA GRADE</div>

This is a paraphyletic grade of New World Lecythidaceae that has the *Bertholletia* clade nested within it (Fig. 2A–B).

Figure 1 shows relationships of worldwide members of the Lecythidaceae clade, whereas Figure 2 shows relationships of the New World taxa. The most recent phylogenies (Mori et al. 2007; Huang et al. 2015; Fig. 1, 2A) support the hypotheses that the actinomorphic-flowered genera *Grias*, *Gustavia*, and *Allantoma*, the tubular zygomorphic-flowered *Cariniana*, and the staminal zygomorphic-flowered *Couratari*, and *Couroupita* are monophyletic and correspond to the genera as circumscribed by Prance and Mori (1979) and Mori and Prance (1990). These conclusions are based on both morphological and molecular data (Huang et al. 2015; Mori et al. 2015).

The clades are discussed in the order they appear on the most recent phylogenetic trees (Figs. 1–2B), but bear in mind that relationships among the clades are not well resolved.

Grias **clade** (99% BS [Mori et al. 2007]; Figs. 1, 3E, 5B; Map 7)

This clade is sister to the *Gustavia* clade. The 11 species in this clade range from Belize to central Peru (Prance & Mori 1979; Clark & Mori 2000; Cornejo & Mori 2010, 2011, 2012b; Mori et al. 2010). Most of the species are associated with the valleys and slopes of the Andes in southwestern Colombia and northwestern Ecuador but two, *G. neuberthii* J.F. Macbr. and *G. peruviana* Miers, occur in Amazonian Colombia, Ecuador, and Peru. *Grias cauliflora* L. is found mostly in Central America but also occurs in Jamaica where it was first described. *Grias peruviana* is disjunct between coastal Ecuador and Amazonian Ecuador and Peru.

Gustavia **clade** (87% BS [Mori et al. 2007]; Figs. 1, 5A, 8; Map 8)

This clade is sister to the *Grias* clade. The 44 species of this clade (Prance & Mori 1979; Mori & Cornejo 2013) range from the Osa Peninsula of Costa Rica (*Gustavia brachycarpa* Pittier) to the state of Pernambuco in the Atlantic Forest of Brazil (*Gustavia augusta*). The genus is especially rich in species in Panama and northwestern Ecuador where as many as eight species have been collected from a grid square. Species of this genus are found in much of Amazonia with the exception of a large area including the llanos of Venezuela and Amazonian Colombia where they are rarely collected. In general, collecting records and species diversity for species of *Gustavia* in much of Amazonia and the Guianas are low—especially in the Guianas and eastern Amazonian Brazil where most of the area has only one to three species per grid square. In a grid square near Manaus, there are four species, and in the Atlantic Forest of Brazil the only species that has been collected is *Gustavia augusta*.

Couroupita clade (100% BS [Huang et al. 2015]; Figs. 1, 2A, 6A–6B; Map 9)

      This monophyletic group is sister to the clade that contains *Cariniana, Couratari, Allantoma*, and the *Bertholletia* clade.

      There are three well-defined species in the *Couroupita* clade. *Couroupita guianensis* has a periamazonian distribution (Granville 1992). In the north, collections of this species have been made in the Guianas, eastern Venezuela, and on the other side of the Andes in the Maracaibo Basin of Venezuela. In addition, numerous collections have been made in western Amazonia in Colombia, Ecuador, Peru, and Brazil. This species is often planted as an ornamental tree and sometimes it is difficult to determine if an individual is a cultivated or native tree. *Couroupita subsessilis* Pilg. runs along the Amazon River from eastern Amazonian Ecuador to near the border between the states of Amazonas and Pará. It has also been collected in the Brazilian state of Acre. This species has not been collected in the states of Pará and Amapá. *Couroupita nicaraguarensis* DC. is distributed from northwestern Nicaragua to coastal areas in northwestern Ecuador.

Allantoma clade (99% BS [Huang et al. 2015]; Figs. 2A, 5B; 10E, Map 10)

      This clade may be sister to the *Cariniana* clade, but we interpret this with caution given that the relationship has less than 50% BS support in the combined analyses of Huang et al. (2005; Fig. 2a). Nonetheless, a sister relationship between *Cariniana* and *Allantoma* was supported by Huang et al. (2008) based on morphological data alone.

      Eight species belong to the *Allantoma* clade (Huang et al. 2008) and two of them, *A. decandra* (Ducke) S.A. Mori et al. and *A. lineata* (Mart. ex O.Berg) Miers, are widespread. The former species, ranging from southwestern to central Amazonia, is primarily found in well-drained lowland forests and the second, ranging from northwestern Amazonia, along the Rio Negro and the Amazon River to near its mouth, prefers riverine vegetation or wet areas along small streams. Species of this clade are limited to the Amazon Basin but are absent in the Guayana lowlands, northern Venezuela, in an area bounded in the north by the Amazon River, in the west by Amazonian Peru and Colombia, and in the east by the Madeira River.

Cariniana clade (<50% BS [Huang et al. 2015]; Figs. 2A, 5C, 10D; Map 11)

      Based on molecular data of Mori et al. (2007; Fig. 1), *Cariniana pyriformis* Miers falls outside of the *Cariniana* lineage, suggesting that the *Cariniana* clade may not be monophyletic. This species was unfortunately not included in the combined analyses of Huang et al. (2015; Fig. 2A), but in all morphological aspects it is clearly a species of *Cariniana* (Huang et al. 2008). A hypothesized sister group relationship between *Cariniana* and *Allantoma* was weakly supported (<50%) by Huang et al. (2015), and was also supported based on morphology alone (Huang et al. 2008).

      The nine species of *Cariniana* (Huang et al. 2008) are found in either lowland forests or savanna habitats on well-drained soils. The overall distribution of this clade (Map 11) is central and southwestern Amazonia, the savanna habitat of central Brazil, and the Atlantic Forest of eastern Brazil. *Cariniana pyriformis* is found in northwestern Colombia, eastern Panama, and the Maracaibo Basin in Venezuela. Two species are disjunct (*C. estrellensis* (Raddi) Kuntze and *C. ianeirensis* R. Knuth) between southwestern Amazonia and the Atlantic Forest of eastern Brazil and one species (*C. pyriformis*) is found in lowlands west and north of the Andes in eastern Panama, northwestern Colombia, and the Maracaibo Basin of Venezuela. Species of *Cariniana* are not adapted to dry thorn scrub (= *caatinga*) of northeastern Brazil and cloud forests.

Couratari clade (BS 81 [Huang et al. 2015]; Figs. 2A, 6M; Map 12)

      This monophyletic group falls in the clade that contains *Cariniana, Allantoma*, and the *Bertholletia* clade, but relationships of the genus are unresolved in Mori et al. (2007) and have <50% bootstrap support in Huang et al. (2015).

There are 19 species in this clade. Mori and Prance (1990) recognized three sections: *Couratari* sect. *Echinata*, *C.* sect. *Guianensis*, and *C.* sect. *Microcarpa*. There is support for retaining sect. *Echinata* but no support for maintaining the other two sections separate from one another (Mori et al. 2007). This clade is found throughout most of Amazonia and the Guianas except for a vast area in the south central and eastern Brazilian Amazon. In addition, two species, the widespread *C. guianensis* Aubl. and the Panamanian/Costa Rican endemic *C. scottmorii* Prance, are found west of the Andes where they occur from northwestern Colombia to the Osa Peninsula and nearby mainland of Costa Rica. In addition, four species have reached the Atlantic Forest where they range from southern Bahia to forests in the state of Rio de Janeiro. These species, *C. asterotricha* Prance, *C. asterophora* Rizzini, *C. pyramidata* (Vell.) R. Knuth, and *C. macrosperma* A.C. Sm., all belong to *Couratari* sect. *Echinata*. *Couratari macrosperma* is found in southwestern Amazonia and in eastern Brazil but further study may reveal that these disjunct populations represent two related species.

BERTHOLLETIA CLADE

Huang et al. (2015) described a species-rich New World clade that includes *Bertholletia*, *Corythophora*, *Eschweilera*, and *Lecythis* as circumscribed by Mori and Prance (1990). The *Bertholletia* clade has low molecular support (63% BS; Fig. 2A–2B). The neotropical genera with actinomorphic flowers (*Allantoma*, *Grias*, and *Gustavia*) and some of the zygomorphic genera (*Couratari*, *Couroupita*, *Allantoma*, and *Cariniana*) are the outgroup of this clade. Huang et al. (2015) concluded that *Corythophora* is monophyletic, *Bertholletia* is embedded in *Lecythis*, and that *Lecythis* and *Eschweilera* are not monophyletic, the former consisting of five and the latter of three clades.

The clades are discussed in the order they appear on the most recent phylogenetic trees (Huang et al. 2015; Fig. 2A) but bear in mind that relationships among and within the clades are not resolved. Do not confuse this clade with the monotypic *Bertholletia excelsa* clade described below.

Lecythis pisonis clade (100% BS [Huang et al. 2015]; Figs. 2A, 4. 6C, 8, 10J; Map 13)
This clade consists of five species that range from Nicaragua to northern Ecuador, The Guayana lowlands, eastern and western Amazonia, and the Atlantic Forest of Brazil. Collections have not been made from north central Amazonia and south of the Amazon River in south central Amazonia. The seeds of species of this clade are edible, so their distribution has been influenced by humans moving plants from one area to another. The seeds of species of this clade are dispersed by bats that eat the basal, fleshy arils and drop the seeds on their way to or at their night roosts. The seed coats are too tough for the bats to open them to eat the embryo.

Lecythis ollaria L. clade (100% BS [Huang et al. 2015]; Fig. 2A. , Map 14).
This clade consists of three species found in northwestern South America in Colombia and Venezuela and in eastern Panama. *Lecythis tuyrana* Pitter is a tall forest tree restricted to eastern Panama and extreme northwestern Colombia. The two other species, *L. minor* Jacq. and *L. ollaria*, are usually collected from dry savannah forests but are found in gallery forests within savanna where they are larger trees. *Lecythis ollaria* is separated from the other two species by the Andes.

Lecythis poiteaui O. Berg clade (72% BS [Huang et al. 2015]; Fig. 2A; Map 15)
This clade consists of five species found in the Guayana lowlands, eastern Amazonia, and the Atlantic Forest. There is a wide dry band consisting of savanna and thorn scrub vegetation in northeastern Brazil that separates the Amazonian and the Atlantic Forest species of this clade. Only one of the species of this clade, *Lecythis lurida* (Miers) S.A. Mori, is disjunct between eastern Amazonia and the Atlantic forest.

***Bertholletia excelsa* clade** (100% BS [Huang et al. 2015]; Figs. 2A, 6G, 9, 10C; Map 16)
    This clade consists only of *Bertholletia excelsa* and is embedded in the *L. ollaria/L. poiteaui/L. chartacea* O. Berg clades (Fig. 2A). Because of low resolution among these four clades, we are not able to determine if this clade should be recognized as a single genus or if the four weakly defined clades should be separated into different genera.

    In Figure 2A, the *L. ollaria* clade is part of the weakly supported *L. ollaria/ L.poiteaui/ Bertholletia excelsa/ L. chartacea* clade. If this clade were circumscribed as *Lecythis* then *B. excelsa* would have to be transferred to *Lecythis* because the type of the genus (*Lecythis ollaria*) was published before any other Lecythidaceae (Dorr & Wiersema 2010a, 2010b). In contrast, if all subclades mentioned in this paragraph were considered as different genera *Lecythis* would be reduced to three instead of the 26 species recognized by Mori and Prance (1990). We hypothesize that future studies will support transferring the monotypic *Bertholletia* to *Lecythis*.

    Today, Brazil nut trees grow throughout much of lowland Amazonia (Map 16). However, the current distribution of this species does not coincide with its original distribution because of dispersal by humans. Ducke and Black (1953) suggested that the overall distribution of *Hevea*, a historically important source of rubber, more-or-less defines the Amazonian hylaea, and Henderson (1995) defined the lowland Amazon Basin as the area below 500 m elevation. Eva and Huber (2005) defined the Amazon Basin based on hydrological, ecological, and biogeographical data. They recognized a large central Amazon basin surrounded by four peripheral areas, the Andes, Planalto, Gurupi, and Guayana subregions.

    There are, however, large areas in southwestern Amazonia and another running east to west beneath the Guianas without collections. The linear series of collections along the Tapajós and other rivers indicate that Brazil nut trees are planted along rivers where humans cultivate the trees for their edible seeds. Maps of *Bertholletia excelsa* in Thomas et al. (2014) can be consulted for a more detailed discussion of the distribution of this species in both present and past times. The localities on their maps are based on herbarium collections and observations whereas our maps are based only on herbarium specimens. Because there is little possibility for misidentification of this species. The Thomas et al. (2014) maps give a better idea of the current distribution of the Brazil nut but make it difficult to know what trees are there because they are cultivated.

Figure 4. Zygomorphic flowers of the *sapucaia* tree (*Lecythis pisonis*) being pollinated by female carpenter bees (*Xylocopa* sp.). The bees are gathering sterile pollen from the inside of the androecial hood while fertile pollen of the staminal ring is placed on their dorsal surfaces. The sterile pollen is fed to their larvae and the fertile pollen is rubbed off onto the stigmas of other flowers on other trees visited thereby pollinating the flowers. Painting by M. Rothman.
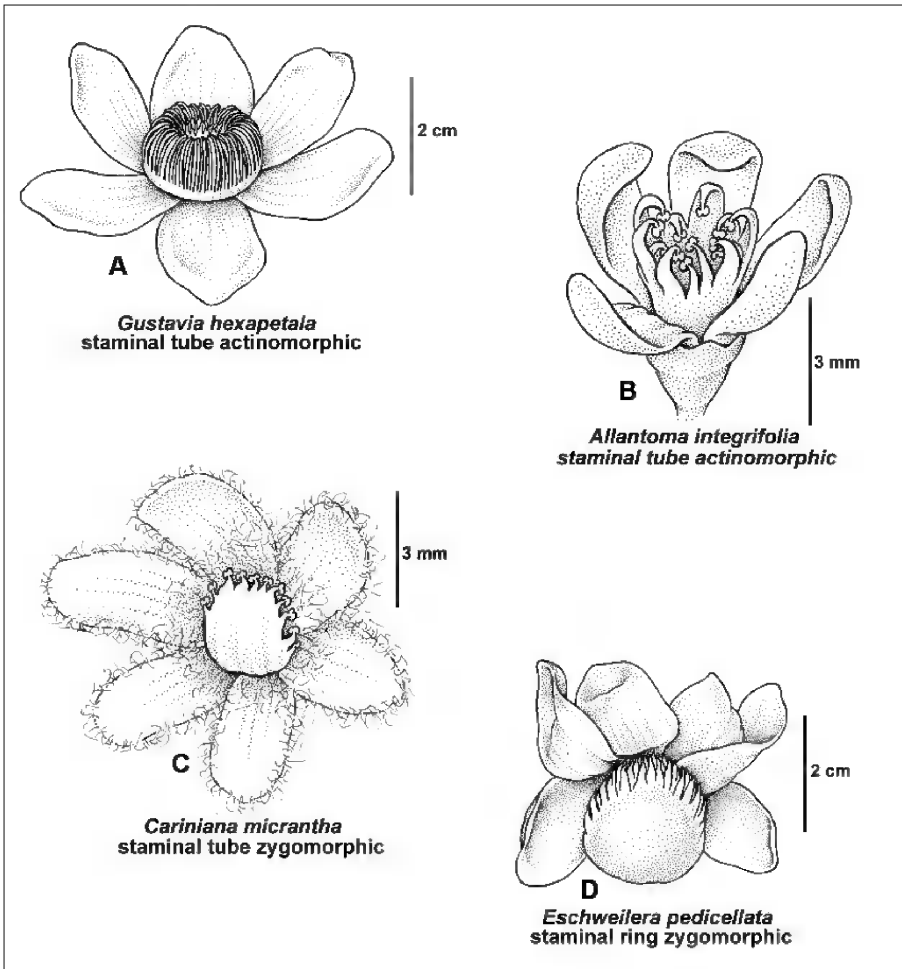
Figure 5. Examples of floral symmetry in the New World Lecythidaceae. A. *Gustavia* type, the androecium is relatively thin and actinomorphic and the stamens are erect, and inserted around the rim of the staminal tube (only in *Gustavia*). B. *Allantoma* type, the androecium is fleshy and actinomorphic and the stamens are reflexed and inserted on the inside and around the rim of the staminal tube (found also in *Grias*). C. *Cariniana* type, the androecium is membranous, the staminal tube is prolonged on one side, the stamens are not reflexed and are inserted around inside of the staminal tube and along its margin (only in *Cariniana*). D. *Lecythis* type, the androecium is fleshy, staminal tube absent, the stamens erect, arising from a staminal ring (found also in *Couroupita, Couratari, Corythophora,* and *Lecythis*). Drawings by B. Angell.
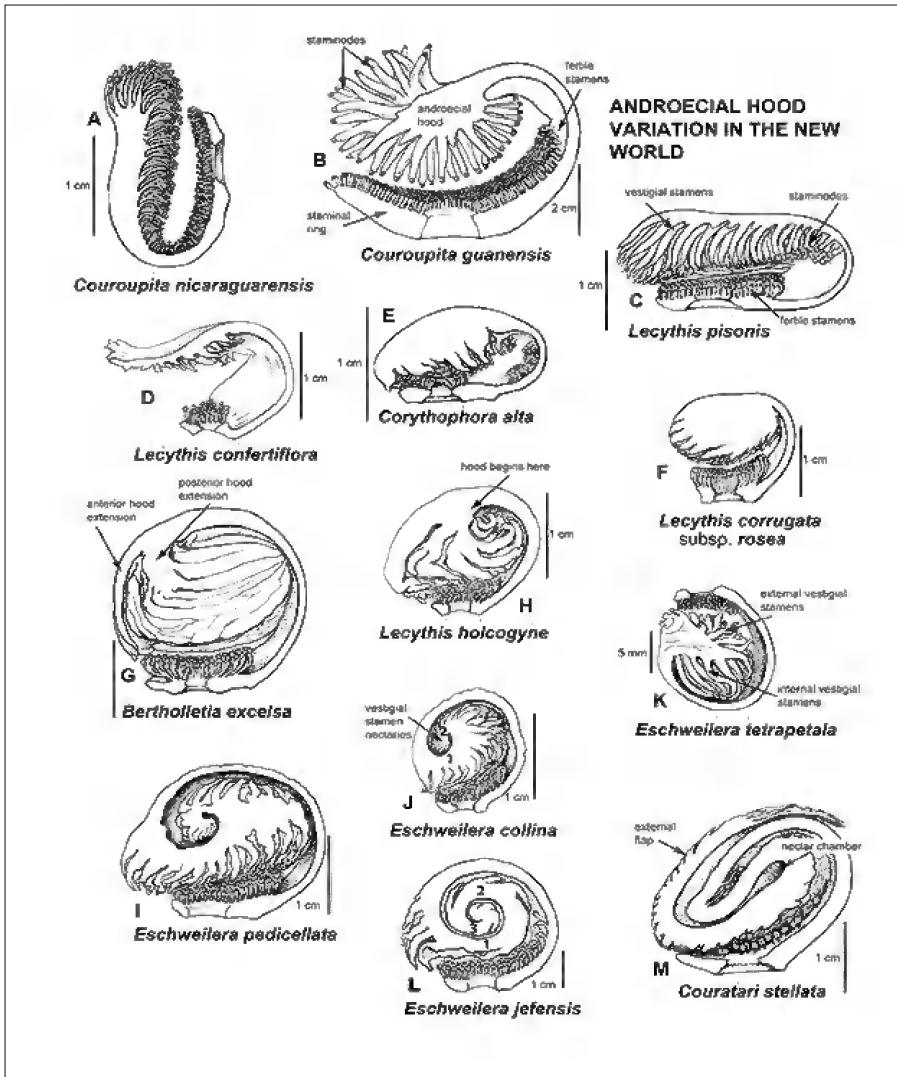
Figure 6.   Variation of the androecium of staminal ring zygomorphic-flowered species of New World Lecythidaceae.   The least complex androecium among the staminal ring zygomorphic genera is *Couroupita nicaraguarensis* (Fig. 6A) and the most complex is represented by *Couratari stellate* (all species of *Cariniana* have an external flap, Fig. 6M).   The numbers in 6J and 6L indicate 2-coiled and 3-coiled androecial hoods, respectively.   Drawings by B. Angell (E–F, H–L) and H. M. Fukuda (G, M).
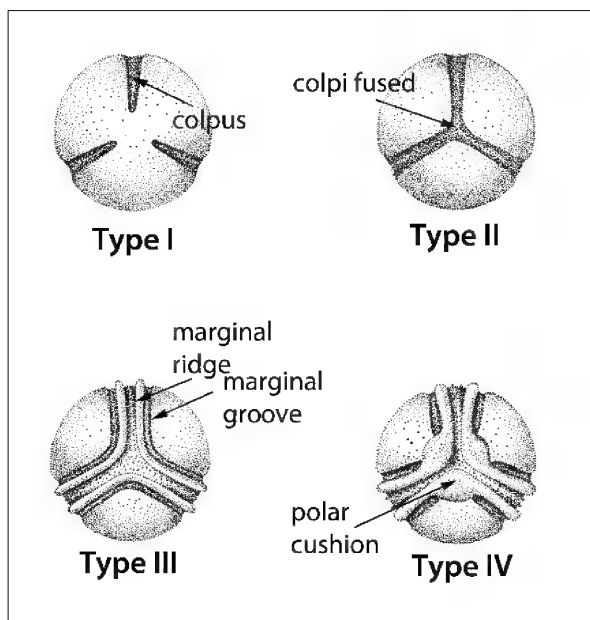
Figure 7. Comparison of the pollen of the Lecythidaceae clade. Type I. Tricolpate pollen found in the Napoleonaeaceae, Scyopetalaceae, Lecythidaceae subfam. Foetidioideae, and Lecythidaceae subfam. Lecythidoideae (the colpi do not fuse at the poles of the pollen grains). Type II. Syntricolpate pollen found in some species of subfam. Barringtonioideae (the colpi fuse at the poles of the pollen grain). Type III. Syntricolpate pollen found in some species of the subfam. Barringtonioideae (the colpi fuse at the poles of the pollen grains and marginal ridges and grooves are present), Type IV. Syntricolpate pollen found in some species of the subfam. Barringtonioideae (the colpi fuse at the poles of the pollen grains and marginal ridges, marginal grooves, and polar cushions are present). Pollen Types III and IV are good indicators of the presence of species of subfam. Barringtonioideae in the fossil record. Adapted from Tsou, 1994).

Lecy*this chartacea* clade (76% BS [Huang et al. 2015]; Figs. 2B, 6H; Map 17).

        This clade consists of at least 11 species found throughout the Amazon and with one species in northwestern Colombia and eastern Panama into Costa Rica (*Lecythis mesophylla* S.A. Mori). The widespread *L. chartacea* may include more than one species. There are no species of this clade in the Atlantic Forest.

***Corythophora* clade** (100% BS [Huang et al. 2015]; Fig. 6E; Map 18)

        There are four species in this clade, one of which (*Corythophora rimosa* W. Rodrigues) is treated as two subspecies (Mori & Prance 1990). *Corythophora rimosa* subsp. *rimosa* has green petals and is restricted to a small area in central Amazonian Brazil and *C. rimosa* subsp. *rubra* S.A. Mori has red petals and is found only in Amapá and French Guiana. This genus forms two distinct subclades, one consisting of *C. amapaensis* Pires ex S.A. Mori & Prance and *C. labriculata* (Eyma) S.A. Mori & Prance and the other of *C. alta* R. Knuth and *C. rimosa* (Huang et al. 2015). This clade has been collected in Surinam, French Guiana, eastern Amazonian Brazil around Bélem, Central Amazonian Brazil around Manaus, and northern Amazonian Brazil near the border with Guayana.

Within this area, there are large expanses without collections but we suspect that species of the genus are there but have not yet been collected.

***Eschweilera integrifolia* (Ruiz & Pav. ex Miers) R.Knuth clade** (<50% BS [Huang et al. 2015]; Figs. 2B, 6L; Map 19)

Huang et al. (2015) recovered a clade of *Eschweilera* species that differs from the Mori and Prance (1990) circumscription of *Eschweilera*. At least 15 species belong to this clade which differs from the *E. parvifolia* Mart. ex DC clade (the type of the genus) by having triple-coiled androecia (versus double-coiled androecial hoods) and arils that usually surround the entire seed (versus lateral arils). The latter feature is difficult to see because the aril is present only in fresh specimens of mature seeds (the lateral aril persists but the spreading aril usually disappears when specimens are dried). In addition, more than one-half of the species have pink to reddish petals but white to pale yellow petals are at least found in *E. aguilarii* S.A. Mori, *E. awaensis* Cornejo & S.A. Mori, *E. collinsii* Pittieri, and *E. ovalifolia* [DC.] Nied.).

Species of this clade range from south of the Costa Rican/Nicaraguan border to northern Bolivia. There are also two Amazonian species: *E. andina* (Rusby) J.F. Macbr. is found in western Amazonia paralleling the Andes from Ecuador to Bolivia; and the riverine *E. ovalifolia* ranges from western Amazonia in Bolivia and Peru and from there as far east as central Amazonia. Species circumscriptions in the Andean species of this clade have not been well established; nevertheless the map gives a good idea of the distribution of the entire clade.

***Eschweilera tetrapetala* S.A. Mori clade** (100% BS [Huang et al. 2015]; Figs. 2B, 6K, 10I; Map 20).

This clade includes seven known species. The basal species is the wide-spread *Eschweilera nana* (O. Berg) Miers, which is restricted to savanna vegetation in the Planalto of Brazil, and six other species endemic to forests of southern Bahia, Espírito Santo, and Rio de Janeiro. The species of this clade differs from the other clades of *Eschweilera* by single instead of double or triple androecial hood coils, more than one row instead of a single row of ovules, and basal instead of lateral or spreading arils.

***Lecythis corrugata* Poit. clade** (99% BS [Huang et al. 2015]; Figs. 2B, 6D, 6F; Map 21)

This clade consists of five species, two of which, are divided into subspecies (*Lecythis corrugata* subsp. *corrugata* and *L. corrugata* subsp. *rosea* (Spruce ex O. Berg) S.A. Mori and *L. persistens* Sagot subsp. *persistens* and *L. persistens* subp. *aurantiaca* S.A. Mori). The overall distribution of the clade is Guayanan but it is also found in eastern and central Amazonia south of the Amazon River. The ranges of the *L. corrugata* subspecies overlap near the Essequibo River and subsp. *rosea* also occurs north of the Venezuelan Andes in the Maracaibo Basin.

***Eschweilera parvifolia* clade** (94% BS [Huang et al. 2015]; Figs. 6I–J, 10G–H; Map 22)

The *Eschweilera parvifolia* clade is the most diverse clade of New World Lecythidaceae with approximately 69 species. Only the Old World Barringtonioideae clade with 69 species is as diverse. This figure was calculated by subtracting the 15 species that fall into the *E. integrifolia* clade, the seven species of the *E. tetrapetala* clade (which should be treated as a new genus), and two species now treated as *Lecythis* (*E. congestiflora* [Benoist] Eyma and *E. simiorum* [Benoist] Eyma) from the 83 species listed in Mori and Prance (1990) and then adding the 10 new species described since this monograph was published (Mori 1992, 1995, 2007; Mori & Lepsch-Cunha 1995; Cornejo & Mori 2011). There are, however, many species in this clade that have not yet been described.

Because of the high number of species in the *Eschweilera parvifolia* clade the map shows only the number of collections and number of species in each of the grids where species of the clade occur. Species of the *E. parvifolia* clade share coiled androecial hoods, vestigial stamen nectaries at the apices of the coils (also found in the *Couratari* clade), two locules (infrequently with 4 locules),

and ovules arranged in a single row (Huang et al. 2015) with the *E. integrifolia* clade. This relationship, however, is not supported in phylogenetic studies based on molecular data (Mori et al. 2007; Huang et al. 2015).

The northern most species of this clade, and of New World Lecythidaceae in general, is *Eschweilera mexicana* Wendt et al. from Veracruz, Mexico. There have been no collections of this clade gathered from Belize, Guatemala, or El Salvador. Of the 11 species of Lecythidaceae on the Osa Peninsula of Costa Rica, five belong to this clade (Mori 2007). In Central America, the Osa is the last place where this clade plays a significant role in the ecology of an area of lowland forest (Aguilar et al. 2008). The southern limit of the clade is *E. ovata* (Cambess.) Mart. ex Miers in the androecial tube is relatively thin and actinomorphic, the stamens arise from the rim of the tube and are arched at the apex (only in *Gustavia*).   B. *Allantoma* type, the androecium is fleshy and actinomorphic and the stamens are reflexed and inserted on the inside and around the rim of the staminal tube (found also in *Grias*). C. *Cariniana* type, the androecium is membranous, the staminal tube is prolonged on one side, the stamens are not reflexed and are inserted around inside of the staminal tube and along its margin (only in *Cariniana*). D. *Lecythis* type, the androecium is fleshy, a staminal tube is absent, and the erect stamens arise from a staminal ring (found also in *Couroupita*, *Couratari*, *Corythophora* and *Lecythis*).   Drawings by B. Angell Figure 5.   Examples of floral symmetry in the New World Lecythidaceae. A. *Gustavia* type, the. state of Espírito Santo, Brazil. The most southern Lecythidaceae, however, is *Cariniana estrellensis* from southern Santa Catarina, Brazil.

There is a dry area ranging from Amazonian Colombia into the savannas of Venezuela where species of the *Eschweilera parvifolia* clade are extremely rare. In addition, the large arid area running in a southwestern direction from northeastern Brazil is not rich in Lecythidaceae. The only species of this clade in the Atlantic Forest is *E. ovata* which is also found in southeastern Amazonia.

DISCUSSION

Methodology

A major problem in determining the distributions of New World Lecythidaceae for phytogeographical studies is that collections are not available throughout the ranges of the species under study. Nelson et al. (1990) demonstrated that the collections of Amazonian species of *Inga* are most abundant in areas surrounding institutions with active herbaria or in areas where these institutions have ongoing projects. They also point out that this collecting bias compromises testing hypotheses such as the role that Pleistocene refuges (Prance & Elias 1977) played in the evolution of Amazonian species. Based on collection data taken from herbarium sheets, the highest number of species of Lecythidaceae found in a grid square corresponds to areas where the greatest numbers of specimens have been collected. Map 6 shows that eastern Central America (Costa Rica and Panama), Amazonian Peru, northwestern Ecuador, the Guianas, Manaus, Belém, southern Bahia, Espírito Santo, and Rio de Janeiro are regions with the highest number of specimens collected and the highest number of species recorded.

Like other tropical tree groups, Lecythidaceae are difficult to sample because of the remoteness of species-rich forests, the short time and irregularity of flowering and fruiting, and the work it takes to climb into the canopy to collect specimens. Collections of flowers and fruits from the same individuals are seldom gathered at the same time, so it is difficult to tell if the fruits from one tree belong to the same species as another tree in flower.

Once specimens have been collected, they need to be identified before they are mapped. For the most part, sterile specimens should not be collected as vouchers for DNA material nor as the source of coordinates for mapping because of the high rate of misidentification (Mori 1998). In long-

term ecological studies with marked and mapped trees it is possible to wait for species only known by sterile specimens to flower and fruit but that is difficult and time consuming.

There are problems even with fertile collections of Lecythidaceae. Sometimes specimens with flowers and seeds lose their structure when they are dried over high heat and under excessive tightening of the plant press, thereby destroying the characters needed to identify the collection to species. For this reason, flowers and seeds need to be dried in paper bags under low heat (or preserved in alcohol) and accompanied by images of the taxonomically important parts of the plant (Mori & Prance 1987).

The difficulty of identifying sterile collections of Lecythidaceae, especially *Eschweilera*, makes sterile collections less desirable for species mapping and as vouchers for DNA collections. The simple, alternate leaves of different species of this genus are especially difficult to tell apart. For example, in an inventory of Lecythidaceae in a 100-hectare plot in central Amazonia (Mori et al. 2001) it was difficult to separate *E. collina* Eyma from *E. romeu-cardosoi* S.A. Mori and *E. truncata* A C. Sm. from *E. coriacea* until specimens from these species were gathered in both flower and fruit.

With additional time, more collections are made and the distributions of some species that were once thought to be endemic to small areas are documented to cover much larger areas. As an example, *Cariniana ianeirensis* (Map 25) was published in 1939 based on a few collections made in the vicinity of Rio de Janeiro. Subsequently this species was gathered in Bolivia in 1991 (*Quevado S. 502*) and then in southern Bahia in 2002 (*Fiaschi 1182*). This species is separated by wide expanses of savanna running from the southwest to the northeast through most of the Planalto of Brazil (Map 25). *Cariniana ianeirensis* grows as a tall tree in forests or as smaller trees in open areas on rocky slopes in the states of Rio de Janeiro and Espírito Santo (M. Lemes & R. Gribel, pers. comm.). The wide ecological amplitude of *C. ianeirensis* must have made it easier for this wind-dispersed species to migrate between the Atlantic Forest and Amazonian Bolivia.

Many species of Lecythidaceae have not yet received scientific names. For example, Prance and Mori (1979) recognized six species of *Grias* in the treatment of the genus in their Flora Neotropica monograph. Recent botanical exploration of the slopes and valleys of the Andes of northwestern Ecuador and southwestern Colombia has yielded six additional species added to these genus (Clark & Mori 2000; Cornejo & Mori 2010, 2011, 2012a, 12b; Mori et al. 2010).

Describing new species of tropical trees based on a finite number of collections from a seemingly infinite number of trees causes problems for defining new species. This slows down the process of publishing new species because taxonomists need to understand what characters separate new species from species already described. Most of the time, collections of new species and their closest relatives are not informative enough to determine the differences that distinguish new species from others that have already been described, a process that may take years to resolve. Bebber et al. (2013) determined that 1855 new species of flowering plants were published annually between 1970 and 2011. They calculated the average lag time between the first collection and publication of a new species took 35 years. A population of what one researcher ("a lumper") calls a species may be interpreted as several species by another researcher ("a splitter"). For example, Dugand (1947) prepared a plate of fruit variation of *Lecythis minor* in which it first appears as if fruits from three species of *Lecythis* were illustrated on the same plate. However, the fruits were gathered from trees in proximity to one another in northwestern Colombia as well as from trees Dugand believed to represent the same species. We have seen the same variation in other species of Lecythidaceae to such an extent that fruits from a single tree of *Allantoma lineata* are variable enough to lead a splitter to describe several species based on fruits from the same tree (Prance & Mori 1979).

Changes in the identification of specimens need to be annotated on the herbarium sheets and the new names entered into a database. In addition, secondary material (e.g., DNA, pickled flowers and fruits, wood specimens, images, etc.) associated with herbarium specimens need to be correctly labelled on the specimens and corrected in the database. As an example, until recently two related species of *Lecythis* (identified as *Eschweilera congestiflora* [Benoist] Eyma and *E. simiorum* [Benoist] Eyma) were archived in the herbarium of The New York Botanical Garden. These two species, if left in *Eschweilera*, cause problems with the herbarium sheets and secondary specimens they voucher (i.e., if this is not done the herbarium sheets and all secondary collections will be misidentified). Likewise, phylogenies will have two species of *Eschweilera* embedded in *Lecythis* (Fig. 2A) and the two species will be mapped as *Eschweilera* instead of *Lecythis*. This problem goes beyond a single herbarium because similar changes have to be made on duplicate specimens and subsidiary objects archived in other herbaria. For the most part, trained herbarium staff are too few to keep up with this time-consuming work.

Interpreting biogeographic patterns depends on phylogenies with resolved and dated trees at the species level. Unfortunately, published phylogenies of Lecythidaceae (Mori et al. 2007; Huang et al. 2015) are not well resolved and have not been dated. In addition, it is difficult to understand the abiotic causes leading to the evolution of species without knowing when events, such as the formation and disappearance of large, inland Amazonian wetlands (such as the Lake Pebas system, Sacet 2014), took place. The resolution problem might be corrected when cladograms based on more species as well as more genes are used, but this is not guaranteed because missing links, caused by extinct and uncollected species, might cause incorrect interpretations of phylogenies. For example, *Lecythis poiteaui* is bat-pollinated (Mori et al. 1978) and was recovered as sister to the bee-pollinated *L. prancei* S.A. Mori (Mori et al., 2007). When another bat-pollinated species (*L. barnebyi* S.A. Mori), was added to the analysis ((Huang et al. 2015) it negated the sister relationship between *L. prancei* and *L. poiteaui* (Fig. 2A).

Ecology of New world Lecythidaceae

Trees of *Bertholletia excelsa* occur most frequently in formerly disturbed *terra firme* forests that develop on well-drained soils. Murça-Pires and Prance (1977) pointed out that *Eschweilera coriacea* (as *E. odora*), and *Lecythis idatimon* (as *L. amara* Aubl.) prefer *terra firme* forests. Mitchell and Mori (1987) demonstrated that even slight variations of altitude in *terra firme* forests make a difference on species distributions. For example, *Corythophora rimosa* and *Eschweilera micrantha* (O. Berg) Miers prefer ridge tops, and *Lecythis corrugata* and *Eschweilera coriacea* prefer the slopes and bottoms of hillsides in the forests of central French Guiana. In a study of the non-flooded forests of central Amazonian Brazil, 37 species of Lecythidaceae were found among the 7,791 individuals of Lecythidaceae documented in a 100-hectare plot of *terra firme* forest, indicating how important the Lecythidaceae are in that habitat (Mori et al. 2001). Approximately 70% of the New World species of Lecythidaceae are found in lowland, non-flooded forests.

Species such as *Allantoma lineata*, *Couratari gloriosa* Sandwith, *Couratari tenuicarpa* A.C. Sm., *Couroupita subsessilis*, *Eschweilera albiflora* (DC) Miers*, E. ovalifolia*, *E. parvifolia*, *E. tenuifolia* (O. Berg) Miers, *Lecythis pneumatophora* S.A. Mori, and *L. rorida* O. Berg (formerly treated as a synonym of *L. chartacea* by Mori & Prance 1990) prefer wetter areas along rivers or low wet areas within non-flooded forests. A few species of Lecythidaceae, such as *Gustavia augusta*, inhabit periodically flooded forest along the Amazon but are sometimes also found in wet areas within forests or even areas that are never inundated.

Black-water (Parolin et al. 2004) and white-water (Campbell et al. 1986) periodically flooded forests have fewer species than non-flooded forests (Arias et al. 2016) and this observation is confirmed by the small number of species of Lecythidaceae found in these habitats. Lower species

diversity of Lecythidaceae in flood plain forests is probably caused by the difficulty of trees to adapt to both flooding and dry periods during the course of a year, especially when either the wet or the dry seasons are longer and more intense than normal or if extreme flooding or dry periods occur in consecutive years. An example is the prolonged flooding of a *terra firme* forest in central Amazonian Brazil from January to May 1989. In this case, many individuals of Lecythidaceae died in the flooded areas because the trees were weakened by the prolonged lack of oxygen in the soil. Wood-boring beetles attacked the trees and left piles of sawdust at their bases (Mori & Becker 1991) thereby increasing tree mortality of Lecythidaceae.   The skeletal tree trunks along the Rio Cueiras in Amazonas, Brazil demonstrates that even trees adapted to periodic flooding are killed by excessively long periods of flooding, especially if they occur several years in a row (S.A. Mori, pers. obs.).

The most common species of Lecythidaceae found in savanna are *Eschweilera nana, E. subcordata* S.A. Mori, *L. minor, L. ollaria, L. schomburgkii* O. Berg, *L. brancoensis* (R. Knuth) S.A. Mori, and *L. schwackei* (R. Kunth) S.A. Mori. The *cerrado* biome of the Planalto of Brazil is a type of savanna that covers two million km^2 in Central Brazil. This vegetation type has been estimated to harbor as many as 6,429 to 10,500 species of vascular plants, of which 35% are endemic (Ratter et al. 2006; Fiaschi & Pirani 2009). Species of plants confined to *cerrado* have been estimated to be less than 10 mya old (Pennington & Lavin 2015) so it is likely an area of recent flowering plant diversification. Like many species of trees in the *cerrado, E. nana* is a small tree with thick bark and a relatively thick seed coat, both of which protect it from periodic savanna fires (see "Atlantic Forest") for additional discussion of this species).

Species of Lecythidaceae occur in the cloud forests of the Andes of South America (e.g., *Eschweilera antioquensis* Dugand & Daniel and *E. sessilis* A.C. Sm.), eastern Panama (e.g., *E. jacquelyniae* S.A. Mori), and the coastal mountains of Venezuela (e.g., *E. perumbonata* Pittier). About five species of *Grias* grow in cloud forests. For the most part, only species of *Grias* and *Eschweilera* have been able to adapt to the cool, wet conditions of cloud forests. Because they are difficult to collect, many cloud forest species of the latter genus represent new species. Species of Lecythidaceae do not occur in higher vegetation types such as *páramo*.

Sometimes species of the same genus occur in adjacent flooded and *terra firme* forests; for example, *Allantoma lineata* grows mostly along periodically flooded rivers while *Allantoma decandra* (Map 10) is found in non-flooded forests.   The former is water-dispersed with seeds possessing a vestigial unilateral wing and a corky seed coat, and the second is wind-dispersed with seeds possessing a well-developed unilateral wing (Ducke 1948). When the seeds of *A. lineata* are ripe they fall into the water and are carried downstream by river currents. The seeds survive in water for at least three months without losing their ability to germinate (Prance & Mori 1979).

Some of today's Amazon riverine species may have pre-adapted to wet habitats while growing in hypothesized marshlands surrounding Lake Pebas (Sacet 2014).   The Purus Arch in Central Amazonia started to erode about 11.8 mya and, because of continued erosion, the Amazon River reached its current configuration at about 2.4 mya (Figueredo et al. 2009). Caputo and Amaral Soares (2016), however, claim that the subsidence of the Gurupá Arch in the late Miocene had the most impact of the change of the Amazon River from the east to the west. During this time, plant species, such as *A. lineata* and those cited by Kubitzki and Ziburski (1994), became established along the banks of the newly formed periodically flooded Amazon River and its tributaries. The complexity of wetland habitats and their association with the Andean uplift (Hoorn 1993; Hoorn et al. 2010, 2017) most likely had an important role in the evolution of Amazonian Lecythidaceae as well as other plants.

Today, individuals of *Allantoma lineata* are common along rivers from northwestern Amazonia to the mouth of the Amazon (Map 10). We suggest that this species lost the unilateral seed wing and developed a corky seed coat as an adaptation to water dispersal. In contrast, *terra firme* species of *Allantoma* have winged seeds that facilitate dispersal by wind as do most species of *Cariniana* (Fig. 10D) and *Couratari* (Fig. 10F) but the species of these genera have not lost their seed wings even though several species of *Couratari* (*C. riparia* Sandwith and *C. tenuifolia*) are riverine species.

We hypothesize that *Allantoma lineata* first evolved in wet areas in northwestern Amazonia and from there dispersed downstream to near the mouth of the Amazon River. Even though back currents can carry seeds upstream, it seems unlikely that they could carry seeds upstream far enough to account for the current distribution of this species. It is also possible for fish to carry viable seeds upstream for very long distances (Anderson & Nuttle 2011) but only if the seeds are not masticated. For example, viable seeds are transported for long distances by frugivorous fish such as the *tambaqui* (*Colossoma macropomum*) (Anderson et al. 2011; Araújo-Lima & Goulding 1997) but this fish eats both the pulp of some species and crushes the seeds of other species (Gottsberger 1978). Long distance dispersal of the seeds of *A. lineata* by fish is unlikely because the only parts of the fruit for fish to eat are the embryos of the seeds (the pericarp is woody) so if the seeds are masticated as they pass through their digestive tracts they no longer germinate. Because it is difficult to identify the macerated seeds of *A. lineata* we have not seen reports of predation by fish of this species. On the other hand, the riverine *Gustavia augusta* (incorrectly reported as *G. speciosa* (Kunth) DC.) possesses hard seed coats embedded in pulp that have been reported to be dispersed by fish that eat the pulp and defecate intact seeds (Lucas 2008).

Although some species of Lecythidaceae have adapted to flooded forests, cloud forests, and savannas habitats, most of the New World species are adapted to non-inundated lowland rainforests. Kubitzki (1997) pointed out that biodiverse genera of flowering plant families often include widespread difficult to identify species found in lowland forests. In general, Lecythidaceae that occur in dry and flooded habitats have strong habitat selection (Sexton & Dickman 2016) and are less difficult to identify than species of widespread lowland rain forest species (Kubitzki 1977; Pennington & Lavin 2015).

Pleistocene refuges

Haffer (1969 2008) and Simpson and Haffer (1978) proposed that speciation of Amazonian forest birds was driven by oscillations between dry and wet periods. During glacial periods, considerable quantities of water were tied up in glacial ice which, in Haffer's model, allowed savannas to expand to such an extent that forested refuges became islands in a sea of savanna. According to this theory, when generalized to plants (Prance 1974), the expansion of dry vegetation in glacial periods fragmented populations of forest-adapted Lecythidaceae leading to allopatric divergence. With the arrival of an interglacial period water became available again and forests expanded such that drier areas were no longer an impediment to the migration of forest plants. When the original populations came together again they were: (1) not morphologically changed enough to be treated as separate species, (2) morphologically different but retained the ability to interbreed thereby creating hybrids, or (3) morphologically distinct enough to be recognized as new taxa.

The Pleistocene refuges hypothesis was originally supported in both studies of plants and animals (Simpson & Haffer 1978; Prance 1982, 1987). However, based on geological and paleoecological data, others challenged the hypothesis (Colinvaux et al. 1996, 2001). These authors claimed, "All geological data from Amazonia imply continuous humid weathering throughout late Tertiary and Quaternary times, with all claims for arid land processes shown to be in error." In addition, they noted, "no pollen data suggest increased coverage of savanna in glacial times." Endler (1982) added, "...many of the assumptions of the refuge hypotheses are not justified" and "The

current distributions are consistent with geographic divergence and adaptation to present day ecogeographic factors." Recent studies of Pleistocene vegetation changes have demonstrated that oscillating water cycles in Amazonia did occur over the last 45,000 years, but they concluded that lowland wet forest did not change to large expanses of savanna during glacial periods (Bush 2017; Wang et al. 2017).

In contrast to the idea that there were no major changes in the extent of savanna during the Pleistocene, a study by Hammen and Absy (1994) found that some forests were replaced by savannas during interglacial periods. Hoorn et al. (2017) found that the presence of grass pollen suggest that dryer vegetation types were present from the late Miocene to Pleistocene. They emphasized that grass pollen percentages were much more common between 2.6 and 0.8 mya than they are today. Another question is why do biologists generally agree that forest expanded during interglacial periods and savannas became more prominent in glacial periods in Africa (Baker 2008)? It seems unlikely for forest plants and savanna plants of the Amazon to respond differently to the same environmental cues as those of tropical Africa. These studies support the idea that at least some areas of savanna and dryer forests replaced wet forests during glacial periods suggesting that the Pleisocene refuge hypothesis may have merit after all.

Prance (1974, 1987) recognized 8 Pacific coast, three Atlantic Forest, and 15 Amazon/Orinoco/Guayanan Pleistocene refuges. Even if these forest refuges did exist, they were not absolute barriers to the migration of Lecythidaceae because: (1) forests and savannas, as they do today, formed a mosaic of these two vegetation types and that would have facilitated movement from one forest refuge to another; (2) some species of Lecythidaceae, such as *Cariniana estrellensis* (Leite 2007), would have been able to move from one forest refuge to another by migrating along gallery forests; and 3) some species, such as *Cariniana ianeirensis* and *Couratari macrosperma*, prefer wet forested areas but can also tolerate dryer habitats.

In summary, distributions of New World Lecythidaceae do not support or negate the Pleistocene refuge hypothesis. Current distributions sometimes coincide with one or more places that have been hypothesized to be plant refuges (e.g., in the Guayana and Imataca refuges of the Guianas, in the Napo and East Peru refuges of western Amazonia, and the Chocó refuge of Eastern Panama and northwestern Colombia along the Pacific coast. Because there are so few species of New World Lecythidaceae in dry forests and savannas and their pollen grains are so similar to those of many other plant families it will be difficult to use this family to test the Pleistocene refuge hypothesis.

Two inexplicable distributions

Asteranthos brasiliensis (Map 3) is native in north central Amazonian Brazil and southern Venezuela where it grows in periodically flooded forests on white sand along the Negro and Orinoco river basins. This species has been treated as belonging to Lecythidaceae subfam. Napoleonaeaoideae (Prance & Mori 1979), as the monotypic family Asteranthaceae (Knuth 1939b), and most recently as a member of the Scytopetalaceae (Tsou 1994; Appel 1996, 2004). The latter placement is based on both molecular and morphological data (Morton et al. 1997, 1998), which make a strong case for the relationship between the Amazonian *A. brasiliensis* and the African species of Scytopetalaceae (Tsou 1994a; Apple 1996, 2004; Morton et al. 1997; Mori et al. 2007). There are no other species in the Lecythidaceae clade that share the combination of a corona derived from petals and ruminate endosperm as do *A. brasiliensis* and genera of the Scytopetalaceae. Although the origin of the corona is debated, Ronse de Craene (2011) argues that "In Napoleoneae (= Napoleonaeaceae) and Scytopetaloideae (= Scytopetalaceae), including *Asteranthos*, the petals are transformed into a plicate corolla closely linked to the androecium." Frame and Durou (2001) also interpret the showy corona of the flower of the related *Napoleonaea* as being derived from modified petals.

The wide disjunction between *A. brasiliensis* in central Amazonia and other Syctopetalaceae in western Africa is difficult to explain. This species has a single-seeded fruit dispersed by water aided by a calyx with a rim that keeps the fruit afloat. Thus, this disjunction might have been caused by long distance water dispersal from Africa to central Amazonia via sea embayments along the current Amazon and Essequibo Rivers (Frailey et al. 1988; Hovikoski et al. 2007).

The other disjunction is that of *Petersianthus* of the Barringtonioideae. One species, *Petersianthus africanus* (Welw. ex Benth. & Hook. f.) Merr., is found in Africa and the other, *P. quadrialatus* Merr, is limited to the Philippines. The numerous stamens with long filaments, inferior ovary, long style, and syntricolporate pollen suggests that this genus belongs in the Barringtonioideae but this needs confirmation because neither of the species have not yet been included in a molecular phylogeny of the Lecythidaceae clade.

Lecythidaceae and Gondwanaland

Distributions similar to those of the Lecythidaceae clade (Map 1) are sometimes explained as derived from widespread ancestral populations separated by the breakup of Gondwanaland (Raven & Axelrod 1972). As a matter of convenience, we include what is now Southeast Asia as part of Gondwanaland, a concept supported by Ridd (1971, 1972) but challenged by Stauffer and Gobbett (1972). Beaulieu et al. (2013) provide a useful literature review of this topic.

In addition to Lecythidaceae, other tropical tree families, such as Annonaceae, Bombacaceae, Burseraceae, Byttneriaceae (formerly part of Sterculiaceae), Cochlospermaceae, Combretaceae, Ebenaceae, Erythroxylaceae, Flacourtiaceae, Hernandiaceae, Hugoniaceae, Icacinaceae, Ixoxanthaceae, Lauraceae, Meliaceae, Memecylaceae, Monimiaceae, Myristicaceae, Ochnaceae, Olacaceae, Proteaceae, Putanjivaceae, Sapotaceae, Stemonuraceae, Simaroubaceae, and Theaceae have similar distributions (Heywood & Brummit 2007). This does not include families that are found today only in South America and Africa (e.g., Cecropiaceae and Chrysobalanaceae), families that appear only in South America and Southeast Asia (e.g., Symplocaceae), families that are widely distributed such as the Fabaceae (Heywood & Brummit 2007), families dominated by herb and shrub growth forms, and families represented by a few species disjunct between Africa and South America (e.g., *Sacoglottis* of the Humiriaceae, *Erismadelphus exsul* Mill. Br. and *Korupodendron songweanum* Litt & Cheek of the Vochysiaceae). This list indicates that there are many flowering plant tree families common to Central and South America, Africa, and Southeast Asia—but relatively few families that share species only between South America and Africa or between South America and Southeast Asia.

Gondwanaland presumably started to separate in the Jurassic, and Rufel et al. (2016) state that South America and Africa separated between 110–80 mya and the final connections between South America, Antarctica, and Australia were severed in the Cretaceous 55–41 mya. Using these dates, a mid-Cretaceous appearance of flowering plant families could have taken place before the break-up of Gondwanaland. As of yet, there are no phylogenies of the Lecythidaceae clade that support or negate this hypothesis.

In the early Cretaceous, some mammals evolved dental adaptations needed for feeding on flowering plants (Brusatte & Luo 2016). The sudden appearance of both the flowering plants and mammals in the fossil record of the Cretaceous supports the idea that diversification of both groups may have facilitated coevolution between them. Although Lecythidaceae have few mammal pollinators (all bats), many mammals disperse and/or prey on their seeds.

The origen of at least some flowering plant families has been calculated to be too young to have their distributions impacted by the separation of Gondwanaland (Davis et al. 2002; Ruhfel et al. 2016). In contrast, others conclude that the Gondwanaland break-up explains, at least in part, the

current distributions of some flowering plant families. Some authors suggest that both continental separation combined with long-distance dispersal may explain intercontinental range disjunctions (Barker et al. 2007; Mennes et al. 2015). Sanmartín and Ronquist (2004) studied the biogeography of animals and plants of the southern hemisphere and concluded that some of the distributions may have been caused by Gondwana separation combined with long-distance dispersal; with long-distance dispersal playing a more significant role in plants than it does in animals.

Interchange between Old and New World Lecythidaceae

Old World Lecyythidaceae subfam. *Barringtonioideae* (= barringtonioids) and New World species of *Grias* share many morphological features. These characters are pachycaul growth forms; large leaves clustered at the ends of stems in many but not all species of either; a calyx that has well-defined lobes (only in *G. neuberthii* in the New Word) or, more frequently, a fused calyx that covers the bud and splits into irregularly shaped lobes at anthesis (ca. 60% of the species of *Barringtonia*, Payens 1967; Prance 2012); the presence of a ring nectary at the summit of the ovary (most barringtonioides and some *Grias*); pendulous ovules attached at the apex of the ovary in all species of both genera (not found in any other genus of New World Lecythidaceae); and universally single-seeded fruits with sparse endosperm. However, the flowers of *Grias* are thick and fleshy; have stamens placed on the inside of the staminal tube instead of only on the rim of the staminal tube; and possess a much shorter style than species of Barringtonioideae. Although *Gustavia* does not share some of the above features with species of the Barringtonioideae both usually have a pachycaul growth form, large leaves, and many stamens attached to the rim of a staminal tube. *Grias* and *Gustavia* and every other New World Lecythidaceae lack the long style of the barringtonioids and possess tricolpate pollen (Erdtman 1952; Muller 1979) whereas the barringtonioids have extremely long styles and syntricolpate pollen (Fig. 7; Erdtman 1952; Muller 1972, 1973, 1979, 1981; Tsou 1994b; Manchester et al 2015).   The co-occurrence of many shared characters between barringtonioids and *Grias* and *Gustavia* could also be explained as symplesiomorphy or homoplasy given that *Barringtonia* is not particularly closely related to the latter two genera based on molecular data (Fig. 1).

We hypothesize that the ancestors of the New World Lecythidaceae originated in Southeast Asia, where all species of Lecythidaceae have actinomorphic flowers (Figs. 3A–D, and migrated from there into Africa (only a few species) and Central and South America or, as discussed above, are the results of the Gondwanaland breakup.   African Napoleonaeaceae and Scytopetaceae have actinomorphic flowers but they are morphologically distinct from other species of the Lecythidaceae clade. In contrast, some of the New World species retain actinomorphic flowers similar to species of *Barringtonia* while others evolved zygomorphic flowers in response to pollination by robust, long proboscis bees, such as carpenter and euglossine bees (Huang 2010).

In addition to the breakup of Gondwanaland, another explanation for the current distribution of Lecythidaceae is long-distance dispersal. Some authors explain disjunct distributions as caused by the ability of plants and animals to disperse over long distances (Queiroz 2014), as is the case with Lecythidaceae. For example, the boreotropical migration route posits that tropical forests in Laurasia and Central America occurred further north into Europe and North America than today (Brusatte & Lou 2016). Davis et al. (2002) proposed that the Malpighiaceae originated in northern South America, repeatedly migrated into North America, and from there dispersed into the Old World via the North Atlantic land connection. They argue that vicariance cannot explain the presence of Malpighiaceae in both South America and Africa because the continents had separated long before the origin of Malpighiaceae. In a study of legumes, Lavin and Luckow (1993) hypothesized that a present-day center of diversity in tropical North America, and with an early Tertiary fossil record from any region there, has a high probability of having sister-group relatives in the Paleotropics and derived relatives in South America.

Fossil syntricolpate pollen similar to species of barringtoniods has been found in Germany from the Middle Eocene (Manchester et al. 2015) and in India from the Tertiary (Muller 1981). In addition, a fossilized barringtonioid fruit was discovered in India from the Tertiary (Mehrotra 2000). The endocarps of some barringtonioids are woody and preserve well; thus, their absence in the fossil record of western Laurasia does not support the idea that Lecythidaceae migrated across Laurasia, along the length of Central America, and into South America. Likewise, easy to identify syntricolpate pollen fossils of Lecythidaceae have not been discovered in the western parts of Laurasia. Nevertheless, it has been shown that northern tropical species are present in Mexico; for example, Wendt (1993) concluded that at least 25% of the tree species of the Mexican lowland rain forests are derived from "northern latitude tropical progenitors."

The dating of animal and plant fossils approximates the dates when taxa first evolved in the form of minimum ages (Beaulieu et al. 2013). For example, mammals are now considered to be older than they were previously thought to be (Brusatte & Luo 2016). Likewise, Hochuli and Feist-Burkhardt (2013) discovered angiosperm-like pollen grains in Switzerland from the Middle Triassic. Yin-Long et al. (1999) proposed that flowering plants dominated landscapes in the mid-Cretaceous as far back as 90 mya and Taylor et al. (2009) indicate that flowering plant fossils were scant before the Cretaceous. If flowering plants did appear in the fossil record that long ago then early lineages of Lecythidaceae could have been separated by the fragmentation of Gondwanaland. The oldest fossils of Lecythidaceae come from the Upper Cretaceous (Table II).

Another migratory route might have been long-distance water dispersal combined with island hopping from Asia along the southern hemisphere to the west coast of South America. Several species of Barringtonia (*B. asiatica* L. Kurz, *B. racemosa* and *B. acutangula*) have fruits with thick, coconut-like husks that facilitate water dispersal (Prance 2012). Today, drift currents flow in directions that make it possible for the fruits of these species to float to the western coast of northern South America and eastern Central America (Strub et al. 1998). If similar currents were present in the distant past then barringtonioids could have migrated from Asia to the Neotropics. However, the forests along this migration route at that time were probably temperate (e.g., *Nothofagus* forests) and, thus, this hypothesis does not support migration of tropical barringtonioid species over wide expenses of ocean under temperate climate conditions.

Although relatively few fossils of Lecythidaceae have been collected, fossil leaves, wood, a single flower, pollen, and fruits of Lecythidaceae have been described (Table II). Because of the difficulty in identifying fossil leaves and wood, previous determination as Lecythidaceae are not as reliable as determinations of fossil syntricolpate pollen, flowers, and fruits. A fossil flower, *Lecythidoanthus kugleri* Berry, was collected from Miocene deposits in Trinidad. In this fossil, the androecial hood is missing, but what remains looks similar to a species of *Couratari* as suggested by Knuth (1939a). One of the fossil fruits, *Barringtonia preracemosa* Mehrotra gathered from Oligocene deposits in India, is a good match for a fruit of *Barringtonia*. Another fossil fruit, *Lecythidopyxion girardotanum* Huertas collected in Cundinamarca, Colombia, is similar to some fruits of extant species of *Eschweilera* but the age of the stratum from which it was gathered was not provided (Huertas 1969). A carbonized Brazil-nut seed was discovered by Roosevelt et al. (1996) at the Pedra Pintada Cave near Monte Alegre in the state of Pará, Brazil. The cave was occupied nearly 11,000 years ago. Such a recent discovery is not useful for hypothesizing when the Brazil nut separated from its ancestors, but can be employed to test hypotheses about the time it took Brazil nut trees to migrate from hypothesized forest refuges to other areas during interglacial periods (Thomas et al. 2014).

Pollen grains offer the best opportunity to date evolutionary changes in Lecythidaceae because of the following: (1) the syntricolpate pollen of the barringtonioids, especially species with

marginal grooves, marginal ridges, and polar cushions (Fig. 7, Types I–III; Muller 1972, 1973; Tsou 1994b; Manchester et al. 2015) are easy to distinguish from Lecythidaceae with tricolpate pollen (Fig. 7, Type I, Muller 1973, 1979); (2) syntricolpate pollen is extremely rare in other extant plant families (e.g., Caryocaraceae and some species of Myrtaceae; Erdtman 1952); (3) the age of syntricolpate pollen has been dated to at least the lower Eocene (Muller 1981) and Martínez-Millán (2010) dated the first Asterids, in which the Lecythidaceae are placed, as at least 89 mya; and (4) the interaction between species of Barringtonioideae and bats could give clues to estimating the age of pollen-type evolution in the Lecythidaceae clade. This assumes that the evolution of the large syntricolpate pollen in this group was the result of selection by large-sized fruit bats (the family Pteripodeae). The oldest known bat fossils were discovered in Europe, Africa, and Australia in the Eocene (Gunnell & Simmons 2005) and pollen of barringtonioids appeared in the fossil record in the Lower Eocene in India (Muller 1981) and the Middle Eocene in Germany (Manchester 2015). The high diversity of both large fruit bats and species of barringtonioids in Southeast Asia is consistent with the idea that large, syntricolpate pollen evolved as the result of coevolution with large fruit bats in the Old World. In contrast, pollinating bats in the New World Phyllostomideae are not nearly as large as their Old World (family Pteripodeae) counterparts (Fleming et al. 2009).

Stroo (2000) studied 130 plant species in 23 different families of which 75 species were bat-pollinated and 55 species were pollinated by other pollinating agents. In this study, the only parameter linked to bat-pollination was the larger size of the pollen grains; for example, in that study Lecythidaceae were represented by three New World species of *Lecythis* (21–29 microns) and four Old World species of subfamily Barringtonioideae (35–65 microns). The pollen size difference hints that larger Old World bat pollinators select plants with larger pollen whereas smaller New World bat pollinators collect smaller pollen. The small sample size used in the analysis requires that this suggestion be studied using a larger sample size of of pollen from all lineages of the Lecythidaceae clade.

Although species of barringtonioids are thought to be bat pollinated, there are only a few studies that have supported this hypothesis. Solomon Raju et al. (2004) observed a large fruit bat, two smaller bats, and birds visiting the flowers of *Careya arborea* Roxb. and concluded that the most efficient pollinators were large bats. Tanaka (2004) reported that moths visit the flowers of the widespread *Barringtonia racemosa* but pointed out that bats do not occur on the island where the study took place. Although we suggest that barringtonioid ancestors colonized the New World there are currently no native species with syntricolpate pollen from there, possibly because large fruit bats are absent in the New World. Among the New World Lecythidaceae only two species, *Lecythis poiteaui* (Mori & Prance 1990) and *L. barnebyi* (Mori & Lepsch-Cunha 1995), have been documented to be pollinated by bats. These relatively small bats (in comparison with Old World fruit bats) seek nectar as a reward when they are pollinating these two species. Inflorescence and floral characters and probable nocturnal flowering (N.P. Smith, pers. comm., 2017) of *L. brancoensis* is shared with the two preceding species suggesting that bats also pollinate this species. As mentioned above, the pollen of these species of *Lecythis* are small compared to the larger pollen grains collected by Old World bat pollinators (Stroo 2000).

Widespread distributions of New World Lecythidaceae

With enough time, suitable habitats, efficient dispersal systems, and the lack of major barriers to migration, some New World Lecythidaceae have achieved widespread distributions. Thomas et al. (2014) estimated the rate of *Bertholletia excelsa* migration which gives an idea of how fast this species of lowland Amazonian forests can migrate from one area to another. They assumed that a forest refuge harboring a Brazil nut population 400 to 500 km from another refuge would take at least 8,000 to 10,000 years to bridge the gap.

Species of *Allantoma* (with the exception of at least *A. lineata*), *Cariniana* (Fig. 10D), and *Couratari* have winged seeds (Fig. 10F) dispersed by the wind after the fruit opens and the seeds fall out. The wings are unilateral in the first two genera and surround the seed in the last genus (Tsou & Mori 2002). *Allantoma lineata* (Fig. 10E) and *Eschweilera tenuifolia* (Fig. 10G) have corky seed coats that facilitate water dispersal. The former species has a vestigial seed wing because it is no longer dispersed by the wind, as are most species of the genus. The latter has lost the lateral aril found in most species of the *Eschweilera parvifolia* clade which are dispersed by animals. *Lecythis rorida* is indehiscent so the fruits drop into the water with the seeds trapped inside. The fruits float away and do not release seeds until the pericarp rots. These last two species have lost their arils because they are dispersed by water and not by aril-eating mammals (e.g., bats).

Figure 8. Greater spear-nosed bat (*Phyllostomus hastatus*) removing a seed with its attached aril from the fruit of a *sapucaia* tree (*Lecythis pisonis*). The bat carries the seed away from the tree to its night roost and the seed is dispersed when it is accidently dropped in flight or when it falls to the ground under the night roost after the aril has been eaten. Painting by M. Rothman.

The *Lecythis pisonis* clade (Map 13) has woody fruits sometimes as large as a human head. This clade possesses fruits that open by an operculum that makes the seeds available for dispersal by bats. The seeds are large and fusiform with well-developed basal, white, edible arils that surround the funicles (Figs. 8, 10J). When the fruit opens, the seeds remain inside. Bats have been documented removing seeds from the fruit (Greenhall 1965) and flying away from the trees, presumably to their night roosts. The bats most likely drop some seeds by accident when flying but most of the time they probably eat the aril and the seeds fall to the ground under their roosts. Bats apparently do not eat the seeds because the seed coat is too hard for them to open to extract the embryo. This clade is

widespread in Amazonia, occupies much of the length of the Atlantic Forest of Brazil, and ranges from northwestern Ecuador to Nicaragua. Because species of this clade are cultivated for their edible seeds, their current distributions have been altered. Today, local people living along the Amazon and Solimões rivers and their tributaries often have trees of the *sapucaia* planted on their property.

Another widespread species of Lecythidaceae is that of the monotypic *Bertholletia excelsa* native to Amazonia (Map 16). However, the distribution of this species does not include two vast areas, one south of the Amazon River in western, central, and eastern Amazonia and another in an east to west band north of the Amazon River running below the southern boundaries of Surinam, Guyana, and Venezuela). An understanding of the distribution of this species is complicated by the fact that Brazil nut trees are frequently planted by humans (Thomas et al. 2014). In addition, the linear distribution of many collections along rivers (Map 16) probably represents trees planted for their edible seeds. Shepard and Ramirez (2011), based on ecological, phytogeographical, genetic, linguistic, and archeological data, make the argument that the original distribution of the Brazil nut was in "northern/eastern Amazonia origen" from where it was subsequently spread by humans to southwestern Amazonia.

Figure 9. Dispersal of the Brazil nut (*Bertholletia excelsa*). The seeds are trapped inside of the fruit because the opercular opening (Fig. 10C) is smaller than the seeds. After the fruits fall to the ground mammals, such as the red-rumped agoutis (*Dasyprocta leporina*) illustrated here, remove the seeds from a fruit by gnawing around the edge of the opercular opening to make it large enough to remove the seeds. Some of the seeds are consumed but others are buried for future consumption and those that are not relocated may germinate and grow into adult trees. Painting by M. Rothman.
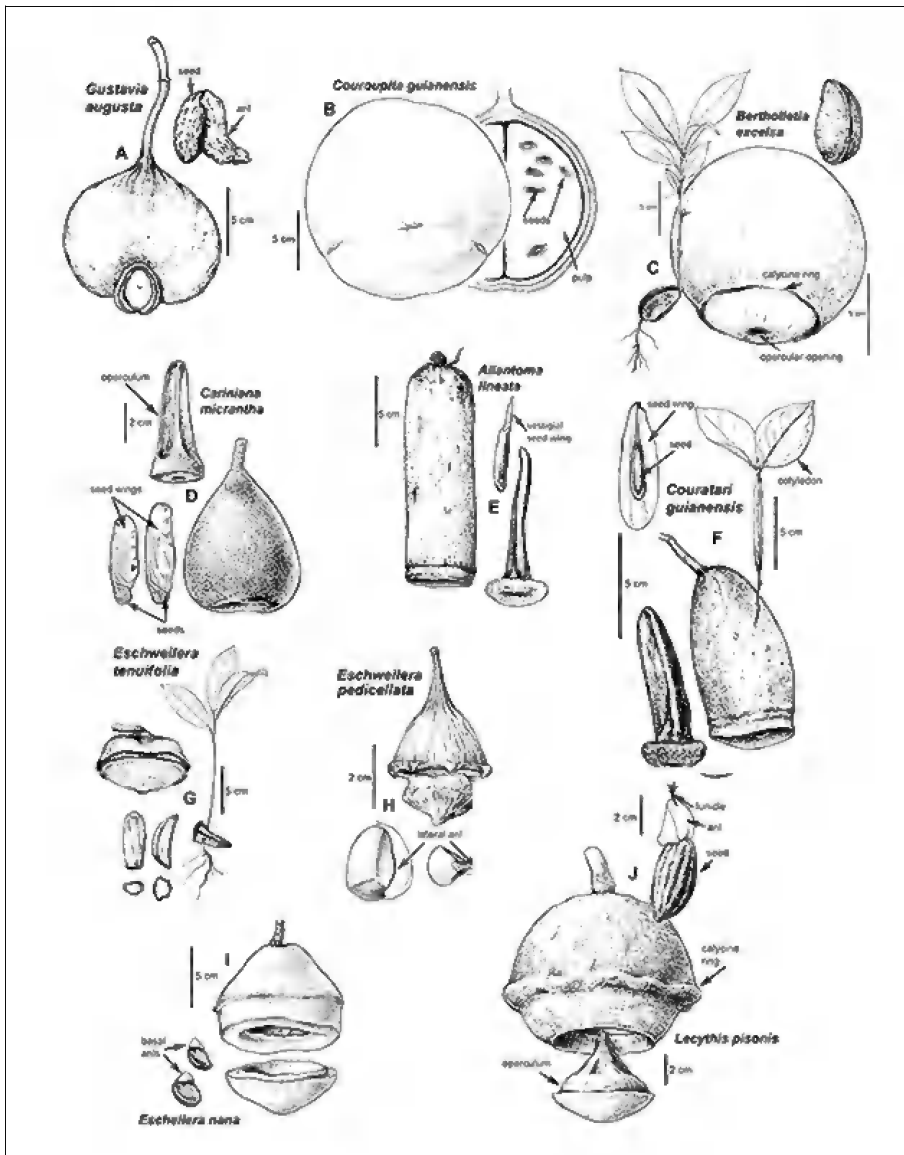
Figure 10. Fruits and seeds of New World Lecythidaceae. The fruits are indehiscent (A, B), secondarily indehiscent (C), or dehiscent (D–J). They are adapted for dispersal by animals (A, B, C, H–J), wind (D, F), and water (E, G). Drawings A, C, E–G. by H. M. Fukuda, D by A. Tangerini, and B, H–J. by B. Angell.

Reátegui-Zirena et al. (2009) concluded that trees they studied in seven populations using molecular data formed a panmictic population. They attributed this to the longevity of the species, an allogamous reproductive system, bee pollinators that can fly at least 20 km in a day (Janzen 1971), and the lack of barriers to seed dispersal by agoutis. As mentioned above, panmictic populations of this species could have also been created by the introduction of germplasm from trees planted by humans.

At maturity the large, round, woody fruits of the Brazil nut fall to the ground with 10 to 25 seeds trapped within the fruits. Agoutis (*Dasyprocta* spp.; Huber 1910), acouchis (*Myoprocta* spp.) and, less frequently squirrels (Tuck Haugaasen et al. 2010, 2012) gnaw open the fruits and remove the seeds from the capsules (Fig. 9). Because the seeds are protected by the woody pericarp and because the boney seed coats (Tsou & Mori 2002) are difficult to gnaw open, only animals with sharp teeth and a strong biting force are able to consume them. Agoutis and squirrels eat some of the seeds and cache others for future consumption. Subsequently some of the cached seeds are forgotten by the animals and it is these seeds that may germinate and grow into the next generation of trees.

Before phylogenies of Lecythidaceae were available, Mori and Prance (1990) hypothesized that *Bertholletia excelsa* was related to species like *Lecythis prancei* and *L. lurida*. This hypothesis was based on the following shared characters of these species with *B. excelsa*: the presence of cuticular papillae on the abaxial leaf blade surface; androecial hood appendages swept or curved inward without forming a complete coil; an anterior hood extension; yellow on the distal end of the androecial hood; and mature fruits that fall to the ground with the seeds inside. However, *B. excelsa* differs by possessing two calyx-lobes, thick woody fruits with such small openings that the seeds are trapped inside when the fruits fall, and seeds with thick and hard seed coats. All of these characters are not found in any other Lecythidaceae. For example, *L. prancei* and *L. lurida* have six calyx-lobes; the indehiscent fruits lack an opening; the pericarp is thin and easy to break open; and the seed coat is membranous and easy to remove.

The relationship of *Bertholletia excelsa* with *L. prancei* and *L. lurida* and other species of the *L. poiteaui* clade is not supported by the most recent cladograms of Huang et. al. (2015) (Fig. 2A). *Bertholletia excelsa* is embedded in the *L. ollaria/L. poiteaui/Bertholletia excelsa/L. chartacea* clade (Fig. 2A). The distributions of both the *L. poiteaui* (Map 15) and *L. chartacea* (Map 17) clades superimpose parts of the *B. excelsa* distribution.

Gustavia sect. *Hexapetala* (as defined by Mori in Prance & Mori 1979), of the *Gustavia* clade, is also widely distributed. The members of this group (*Gustavia hexapetala* Aubl., *G. brachycarpa*, *G. dubia* [Kunth] O. Berg, and *G. longifuniculata* S.A. Mori) possess calyx lobes with inverted y-shaped thickenings on their adaxial surfaces and winged hypanthia not found in other species of *Gustavia*.. Individuals of *Gustavia* with these features are widely distributed in the Guayana lowlands, the northern, eastern and western parts of Amazonia, and west of the Andes from northwestern Ecuador to Costa Rica. *Gustavia brachycarpa* is restricted to the Pacific slopes from central Costa Rica to western Panama, while *G. dubia* occurs on the Caribbean side of Central Panama into the Magdalena River valley of northwestern Colombia, and as far south on the western side of the Andes to northwestern Ecuador. The group is absent from the coastal forests of eastern Brazil as well as from southern Amazonian Brazil. There are no field observations on this group's dispersal biology but the presence of pulp surrounding the seeds and an aril suggests that the dispersal of species in this group are arboreal animals, probably monkeys and/or birds. Pieces found on the ground below fruiting trees indicate that mammals or birds or, perhaps both, are dispersal agents. The pulp surrounding the seeds of *Gustavia superba* (Kunth) O. Berg (not part of sect. *Hexapetala*) is consumed by many different animals (Sork 1977).

Couratari guianensis is distributed in the Brazilian Amazon; the Guayana lowlands; Amazonian Venezuela, northern Bolivia, Peru, Ecuador, and Colombia; and Central America as far north as San José, Costa Rica (Map 12). This species is found both south and north of the central cordillera in Central America. When its winged seeds are ripe, they fall from the fruits and are dispersed by the wind.

Allantoma lineata has a widespread linear distribution along major rivers in Amazonia (Map 10). The seeds of this species drop into the water and are carried downstream by river currents, but other species of this genus have well-developed winged seeds dispersed by the wind.

We conclude that at least some taxa of New World Lecythidaceae have the ability to establish themselves over wide areas regardless of their type of dispersal system. The present distribution of some Lecythidaceae on both sides of the Andes suggests that populations of some taxa were widely spread before the uplift of mountains, and then isolated from one another by the formation of mountain barriers such as the Andes. All of the taxa mentioned in this section are lowland species usually not found over 500 m elevation. Thus, it is unlikely that trans-Andean populations had contact with one another after the uplifted mountains reached higher elevations unless they migrated through mountain passes or along coastal areas when sea levels were lower during glacial periods (Scotti-Saintagne et al. 2013).

High species diversity in central Amazonia (Fig. 24)

The forests surrounding Manaus, Brazil, are rich in overall numbers of species and endemics of tree species, and this is also true for Lecythidaceae (Mori et al. 2001). The high diversity and high endemism is, at least in part, the result of intensive collecting by botanists associated with the *Instituto de Pesquisas da Amazônia*, especially because William Rodrigues, Ghillean T. Prance, Marlene Freitas da Silva, the senior author, and those who worked with them targeted Lecythidaceae for collection in this region over a long period of time. In Map 6, the number of collections and the number of species for each grid square shows that Manaus has the highest number of collections of Lecythidaceae from the New World and twice as many species as any other area of the New World tropics; thus, it is clear that biased sampling hinders phytogeographical studies (Nelson et al.,1990).

Oliveira and Daly (1999) and Oliveira and Mori (1999) agreed that high collection density must be considered but added that some of the increase was caused by the evolution of endemic species *in situ* as well as by species reaching the limits of their distributions in central Amazonia (Map 24). To address the hypothesis, Oliveira and Daly (1999) analyzed the distributions of 2,541 Amazonian tree species found in lowland *terra firme* forests in a 100 km radius surrounding Manaus. They found that 7.1% and 42.2% of the *terra firme* species were endemic or had their limits of distributions around Manaus, respectively. They did the same analysis centered on two other areas with high numbers of collections (Santarém and Belém, both in the state of Pará). In these two localities, the null hypothesis that these two areas have the same proportion of endemics and species with distribution limits as found near Manaus was rejected. This supports the idea that increased endemism and migration from different areas—not just the high number of collections— drive tree diversity in the Manaus area.

Additional support for this idea is provided by a comparison in which the presence of species of Lecythidaceae in central French Guiana (Mori 1991) was compared with the Lecythidaceae of a forest north of Manaus (Mori & Lepsch-Cunha 1995). The following species were recorded from both places: *Corythophora rimosa, Couratari guianensis, C. stellata* A. C. Sm., *Eschweilera collina, E. coriacea, E. grandiflora* Mart. ex DC., *E. laevicarpa* S.A. Mori, *E. micrantha, E. pedicellata* (Rich.) S.A. Mori, and *Lecythis poiteaui.* Ten of the 27 (37%) species in French Guiana also occur in

the Amazonian forest, and four (14.8%) of these species, *C. rimosa*, *E. collina*, *E. pedicellata*, and *L. poiteaui*, reach the end of their distributions in the vicinity of Manaus.

The following species are examples of endemics occurring in central Amazonia within a radius of 200 km around Manaus: *Allantoma integrifolia* (Ducke) S.A.Mori et al. (Map 10), *Corythophora alta* and C. rimosa subsp. rimosa (Map 18), *Couratari longipedicellata* W.A. Rodrigues (Map 12), *Gustavia elliptica* S.A. Mori, *Eschweilera amazonica* R. Knuth, *E. amazoniciformis* S.A. Mori, *E. cyathiformis* S.A. Mori, *E. rhododendrifolia* (R. Knuth) A.C. Sm., and *L. barnebyi*. There are also numerous "endemic" species known from a single location that are not included in this list.

In addition, species from western Amazonian Brazil can also reach or nearly reach the central Brazilian Amazon. In the following list, those species reaching Manaus from western Amazonia are marked with an asterisk while those not marked occur only in western Amazonia: *Allantoma decandra**, *Cariniana micrantha**, *Couroupita subsessilis* (riverine)*, *Eschweilera albiflora** (riverine species), *E. andina*, *E. bracteosa** (Poeppig ex O. Berg) Miers, *E. gigantea* (R. Knuth) J.F. Macbr., *E. itayensis* R. Knuth, *E. juruensis* R. Knuth, *E. laevicarpa**, *E. ovalifolia** (riverine species), *E. rufifolia* S.A. Mori, *E. tessmanii* R. Knuth*, *Grias neuberthii* J.F. Macbr., *G. peruviana* Miers, and *Gustavia macarenensis* Philipson. The rich tree flora of western Amazonia reflects the high alpha-diversity from northern Bolivia to southern Colombia (Saatchi et al. 2008).

The occurrence of high species diversity in central Amazonia could be at least partially explained by the drying out of mega-wetlands in western Amazonia that persisted from at least the middle to the late Miocene (Shephard et al. 2010), the presence of sea embayments, and/or the drying out of hypothesized Pleistocene/Holocene Lago Amazonas that presumably covered large expanses of central Amazonia (Frailey et al. 1988; Mori 1991). Tuomisto et al. (1992), however, have debunked the presence of Lago Amazonas as described by Frailey et al. (1988). Over time, the Amazon Basin has experienced the formation and drying out of wetlands related to the uplift of the Andes (Hoorn et al. 2010), seawater embayments (Hovikoski et al. 2007), or the increase of water that occurs during interglacial periods.

Under this scenario, the breakthrough of the Amazon River to the east between 11.8 and 11.3 mya (Figueiredo et al. 2009) or 9.4 and 9 mya (Hoorn et al., 2017) drained the wetlands and opened central Amazonia to migration of Lecythidaceae from various directions, but especially from western Amazonia and the Guayanan lowland forests. In addition, endemic species could have evolved when satellite populations, isolated on large islands covered with *terra firme* forests, evolved into species distinct from the original populations. A possible example of this is the evolution of the endemic central Amazonian *Lecythis barnebyi* when water barriers separated it from widely distributed *L. poiteaui* (Map 15). Based on our most current phylogeny (Fig. 2B) these species are closely related.

Uplift of the Andes

Speciation of some clades and species of Lecythidaceae was driven by the uplift of the Andes. For example, nine of the 12 known species of *Grias* are endemic to the Andes of northwestern Ecuador and Colombia where they are limited to Andean valleys and slopes (Map 7). Because there were no high mountains before the Andean uplift (Gregory-Wodzicki 2000) the ancestors of the Andean species of *Grias* are assumed to have inhabited low elevations. Today, *G. neuberthii* and *G. peruviana* (usually found at 150 to 800 m altitude) are common along the base of the eastern slopes of the Andes, the latter also appears on the western side of the Andes in Ecuador (Map 7). The broadest distribution of a species in this genus is that of *Grias cauliflora* (Map 7), which occurs at low elevations on the western side of the Andes from northwestern Colombia to Belize with a disjunct population in Jamaica (Map 7). In lower Central America this species has

populations on both sides of the Central American cordillera, but north of Costa Rica the species is only found on the Caribbean side (Map 7). Numerous, more widely distributed species of other families are disjunct between the Pacific and Caribbean slopes in Central America but most of these are also found in other areas of Central and South America (Cornejo et al. 2012; Dick et al., 2005, 2013), as are *Eschweilera coriacea* and *Couratari guianensis* (Map 12).

The endocarps of *Grias cauliflora* have been collected on the beaches of Florida and San José Island, Costa Rica (Ridley 1930; Johnston 1949; Gunn & Dennis 1976). According to Ridley (1930) the seeds remain viable after floating in fresh water for months but perish when they are exposed to salt water. Nevertheless, the presence of *G. cauliflora* in Jamaica seems most likely to be the result of long distance dispersal by water. The fleshy, edible mesocarp and large-sized, single-seeded fruits of this and other species of *Grias* suggest dispersal by mammals that eat the mesocarp. After the pulp is removed by animals, the endocarp and enclosed seed may be secondarily dispersed by water.

Jacaranda copia (Aubl.) D. Don (Bignoniaceae) is found on both sides of the Andes. This species consists of two subspecies: *J. copaia* subsp. *copaia* and *J. copaia* subsp. *spectabilis* (Mart. ex A. DC.) A.H. Gentry. The first is distributed in the Guayana lowlands and the second is widespread in lowland moist and wet forests from Belize to Bolivia. The low genetic variation between the *cis/trans* populations suggests that this disjunction did not arise from the separation of the Amazonian and *trans*-Andean populations caused by the uplift of the Andes (Scotti-Saintagne et al. 2013). These authors hypothesize that the progenitors of the *trans*-Andean population may have migrated around the northern part of the Andes when sea level was lower. Presumably, the exposed area would have been covered by savannas or dry forests. However, most Lecythidaceae are not adapted to savannas or dry forests (see section "Ecology of New world Lecythidaceae"). The broad ecological tolerance of some species of Lecythidaceae could have favored their dispersal through a dry northern dispersal corridor along the Caribbean coast but there are only a few extant species of Lecythidaceae in this region that tolerate dry habitats (e.g., *L. minor*). On the other hand, this and other species of various families may have circumvented Andean barriers by migrating through lowland passes (Scotti-Saintagne et al. 2013). These authors conclude that the trans-Andean distribution of taxa of *Jacaranda copia* is the result of recent events after the uplift of the Andes.

The *Lecythis ollaria* clade (Map 14) includes only three species—two (*L. ollaria* and *L. minor*) adapted to savannas and one (*L. tuyrana*) adapted to wet forests. In this case, it is also possible that the first two species adapted to a dryer climate from a progenitor similar to *Lecythis tuyrana* or *vice versa* but these scenarios are not supported by molecular data (Fig. 2A). *Cariniana pyriformis* (Map 11) is found in the Maracaibo Basin, in valleys in Northwestern Colombia, and Eastern Panama while all other species of the genus are *cis*-Andean (Map 11).

The *Gustavia* clade (Map 8) has high species diversity west of the Andes. Species of this clade are common in inter-Andean valleys and slopes, especially in the area from eastern Panama into northwestern Colombia as far south as northwestern Ecuador. Species of this genus are, however, found all over the Amazon basin but only the widespread *G. augusta* has reached the Atlantic Forest of eastern Brazil.

Gustavia has fewer species in eastern Amazonian Brazil and the Guianas than it does in the Andes. For example, there are only four species in the three Guianas (Mori & Prance 1993), two species in the Flora of Central French Guiana (Mori et al. 2002), and seven species in the Flora of Venezuelan Guayana (Mori & Prance 1999). In contrast, there are 13 species of *Gustavia* in Ecuador (Cornejo & Mori 2012a) and nine species in Panama (Mori et al. 2010), of which only one species is common to both areas. Eastern Panama, the Pacific coast of Colombia, and northwestern Ecuador harbor nearly 50% of the species of *Gustavia* (Map 23).

The *Eschweilera integrifolia* clade (Huang et al. 2015) has many poorly defined cloud forest species ranging from northwestern Ecuador on the slopes and in the valleys of the Andes into Costa Rica. There are only two well-defined species of this clade found east of the Andes in the lowlands of western Amazonia (Map 19): *Eschweileera andina* (with pink to purple petals and androecia) and *E. ovalifolia* (with light yellow petals and androecia). The former occurs along the foothills of the Andes and the latter is found there as well but its distribution extends as far east as the junction of the Negro and Amazon rivers. The two Amazonian lowland species of this clade could have been the ancestors of the Andean species because Andean habitats were not available until after the uplift of the Andes. Once the Andes surpassed 500 meters genetic interchange between the two lowland species and the evolving Andean species may no longer taken place. We assume that triple-coiled androecial hoods and spreading arils were preceded by ancestral species with double-coiled androecial hoods and lateral arils, i.e., the more complex character states are built upon the less complex character states. However, the evolutionary relationship between the *E. parvifolia* and *E. integrifolia* clades have not been supported by molecular based phylogenies (Mori et al. 2007; Huang et al. 2015).

We know that approximately 50% of the species of *Eschweilera* in Central America belong to the *E. parvifolia* clade. On the other hand, there are only the two species mentioned above of the *Eschweilera integrifolia* clade found in Amazonia. It is clear that the *parvifolia* clade dominates throughout the Amazon Basin whereas there are equal numbers of species of the *E. parvifolia* and *E. integrifolia* clades found west of the Andes into Central America.

The Venezuelan Andes have been a barrier to migrations of species of Lecythidaceae into the Maracaibo Basin where only five species of Lecythidaceae are known to occur (*Carinina pyriformis* [Map 11]; *Couroupita guianensis* [Map 9]; the poorly known *Gustavia tejerae* R. Knuth; *Lecythis corrugata* subsp. *rosea* [Map 21]; and *L. minor* [Map 14]). The species found there could have migrated along the coast to the Maracaibo Basin, especially during times when water was tied up in glaciers and more forest paralleled the shoreline than today. On the other hand, these species could have crossed the Andes before the mountains were too high to block their passage into the Maracaibo Basin. It is surprising that both the *Eschweilera integrifolia* and *E. parvifolia* clades, together totaling more than 85 species, have apparently contributed no species to the Lecythidaceae flora of the Maracaibo Basin.

The *Couroupita* clade (Map 9) consists of three lowland species: *C. nicaraguarensis* is trans-Andean, *C. guianensis* is cis-Andean with a peri-Amazonian distribution (Granville 1992), and *C. subsessilis* is cis-Andean and mostly restricted to the banks of the Amazon River and its tributaries. These three species are found in lowland forests from near sea level to about 500 m elevation.

Huang et al. (2015) recovered *Couroupita subsessilis* as sister to the *C. nicaraguarensis*/*C. guianensis* clade (Fig. 2A). The androecial morphology of *C. nicaraguarensis* (Fig. 6A) is the least complex of the three species of the genus. This species has 100% fertile stamens in the staminal ring, progressively fewer fertile stamens along the ligule, and an increased number of staminodes toward the apex of the ligule. At the apex, nearly 100% of the appendages are sterile (Mori et al. 1980). In contrast, *C. subsessilis* and *C. guianensis* lack staminal appendages between the staminal ring and the apex of the ligule (Fig. 6B). The flowers of both *C. subsessilis* and *C. nicaraguarensis* have white petals, golden yellow anthers, and a tendency to have a cleft at the apex of the androecial hood. Based on these observations we hypothesized that *C. nicaraguarensis* and *C. subsessilis* were more closely related than either of these species are to *C. guianensis* but our molecular-based cladogram (Fig. 2A) does not support this hypothesis.

We hypothesize that the uplift of the Andes, including the Cordillera Central of Central America, had a major impact on the speciation of the *Couroupita*, *Grias*, *Gustavia*, and *Eschweilera integrifolia* clades. Bagley and Johnson (2014) point out that lower Central America is geologically complex and, as a result, populations of plants and animals were separated from one other (e.g., isolated on islands and in mountain valleys or by altitudinal differences).

This has resulted in high diversity of Lecythidaceae over a relatively small area in eastern Panama, northwestern Colombia, Pacific coastal Colombia, and northwestern Ecuador. Further south along the Pacific coast there are few, if any, species of Lecythidaceae, and, in Central America, the last significant population of Lecythidaceae to the northwest occurs on the Osa Peninsula where there are five genera and 11 species of the family (Aguilar, et al. 2008). Further to the north, the family becomes less-and-less common with five genera and six species in Nicaragua (Prance & Mori 2001) and only one species, *Eschweilera mexicana* Wendt et al., in Veracruz, Mexico (Wendt et al. 1985). The current distribution of Lecythidaceae indicates that it is a South American lineage that migrated into Central America.

Evolution of species of Lecythidaceae in northwestern South America/eastern Central America was probably driven by the following events: (1) the uplift of the Andes resulting in the evolution of *cis-* and *trans-*Amazonian species, (2) the formation of isolated Andean valleys where ecologically separated populations evolved into new species, (3) adaptation to the high altitudinal habitats of newly formed cloud forests, (4) the formation and inundation of islands before the closure of the Central American land bridge, and (5) the arrival of seeds carried by ocean currents from southeastern Asia to the Pacific coasts of South and Central America. These factors, in combination, contributed to the high diversity of Lecythidaceae in eastern Central America/northwestern South America as well in other plants (Cuatrcasas 1970) and animals (Bagley & Johnson 2014).

It has been suggested that the Andes uplift resulted in the diversification of plant species to such an extent that the coastal forests, valleys, and slopes of the Andes may be more species rich in plants than the Amazon Basin (Henderson et al. 1991). For trees, however, the high *alpha* diversity of Amazonia (up to 300 species over 10 cm DBH per hectare; Gentry 1982; Oliveira & Mori 1999) and the vast forested area of Amazonia make this seem unlikely. West of the Andes Lecythidaceae reach 20 species per grid square (only in Panama) whereas they frequently have over 20 and up to 60 species per grid square (only central Amazonia) east of the Andes in Amazonia (Map 6).

Lowland Guayana Floristic Province

This region is located in the northeastern part of South America bounded by the Atlantic Ocean in the northeast, the Amazon River in the south, the Rio Negro in the southwest, and the Rio Orinoco in the northwest (Mori 1991). The Guayana Highlands (Maguire 1970) are part of the Guayana Floristic Province but not included because there are no Lecythidaceae found at high elevations in the region. In this paper Guayana is used instead of Guiana or Guyana for three reasons: (1) Guyana is the name of a country, (2) the Guianas is a name for the three political units in northeastern South America (Guyana, Suriname, and French Guiana), and (3) two major botanical books, the Flora of the Guayana Highlands and the Flora of Guayanan Venezuela were published before botanists started to use Guiana in reference to this part of South America (Lindeman & Mori 1989).

The best example of a Guayana lowland distribution is the restriction of the 18 taxa of *Eperua* (Fabaceae Subfam. Caesalpinioideae) in the area described in the preceding paragraph (Cowan 1975). This distribution also occurs in species of birds (Haffer 1974; Cracraft & Prum 1988) and reptiles (Dixon 1979). One-third of the species of neotropical Chrysobalanaceae, 24 % of Meliaceae, and 22 % of Sapotaceae occur in the Guayana lowlands (Mori 1991) which suggests that this area harbors about one quarter of the tree species found in the New World tropics.

The *Lecythis corrugata* (Map 21) and *Corythophora* (Map 18) clades as well as individual species of other clades of New World Lecythidaceae (e.g., *Couratari calycina* Sandwith, *C. gloriosa*, *Eschweilera collina*, *E. subglandulosa* [Steud. ex O. Berg] Miers, *L. poiteaui*, *L. congestiflora*, and *L. simiorum*) are endemic to the Guayana Lowlands. In a study of the Lecythidaceae of Central French Guiana, Mori (1991) found that some of the species of Lecythidaceae occurring there reached the western limits of their distributions between the Essequibo River and the boundary between Guyana and Venezuela with only a few species (e.g., *E. sagotiana* Miers) distributed as far west as the mouth of the Orinoco River.

We hypothesize that in the past the distributions of Guayana lowland tree taxa may have been restrained by large inland lakes or epicontinental seas (Frailey et al. 1988; Mori 1991; Bush & Oliveira 2006; Sacet 2014). After the Amazon River broke through the Purus arch and reached its present shape and size some 2.4 mya (Figueredo et al. 2009; Shephard et al. 2010) the newly exposed lake bottoms in western and central Amazonia would have become available for colonization. Although Lake Pebas is well documented (Sacet 2014), Lago Amazonas may not have existed (Tuomisto et al. 1992), at least not in such a massive area.

Contemporary species of the *Lecythis corrugata* clade are confined to the Guayana lowland Floristic Province and adjacent Brazil (Map 21). *Lecythis corrugata* encompasses two subspecies, subsp. *corrugata* in the eastern and subsp. *rosea* in the western parts of the Guayana lowlands (Map 21). The separation of these two subspecies may have been an adaption to dryer forest habitats in the western part of Guayana where subsp. *rosea* occurs. The main differences between the two subspecies are the more coriaceous leaves with striations on the upper surface of subsp. *rosea* and more chartaceous leaves without striations on the upper leaf surface of subsp. *corrugata*. The coriaceous leaves may be an adaptation for water conservation and, if so, the evolution of these two subspecies may have occurred because of ecological adaptation instead of a physical barrier. The border between the two subspecies is more-or-less along the Essequibo River and an embayment along that river may have contributed to the separation of these two subspecies from the original population.

Lecythis corrugata subsp. *rosea* has a widespread distribution in Amazonian Venezuela and north central Amazonian Brazil. It is absent in the savannas of Venezuela, reappears on the southern slopes of the Andes in Venezuela, and is found north of the Andes around Lake Maracaibo (Map 21). The *cis-* and *trans-*Andean populations may have been separated by the uplift of the western Venezuelan Andes and, after the mountains reached an elevation of 500 m altitude, there was no further genetic exchange.

The *Corythophora* clade (Map 18) is currently restricted to the eastern and central parts of the Guayana Floristic Province. Two species of the clade, *C. alta* (with reddish pink petals and androecial hoods) and *C. rimosa* subp. *rimosa* (with green petals and white androecial hoods), are found growing next to one another just north of Manaus. In French Guiana, *C. amapaensis* (with reddish-pink petals and androecial hoods) and *C. rimosa* subsp. *rubra* (with purple petals and white androecial hoods) also grow sympatrically. The sympatric distributions of the two species pairs suggest that the different flower colors may have evolved because of pollinator preferences. The other species, *C. labriculata* (with reddish pink petals and androecial hoods), is endemic to Surinam where no collections of other species of the genus have been collected.

Atlantic Forest (Mata Atlântica)
The forests of the eastern coast of Brazil range from Rio Grande do Norte State to Rio Grande do Sul State. These forests are found in a narrow strip paralleling the coast and ranging in width from several km in the north to 120–160 km in the south (Smith 1962; Bigarella et al. 1975; Andrade-Lima 1977; Mori 1989; Fiaschi & Pirani 2009). Although this phytogeographic domain is

relatively small (1.5 million sq^2 km), it is estimated to have at least 14,000 (Zappi et al. 2015) to as many as 20,000 (Fiaschi & Pirani 2009) species of vascular plants. Because of high species diversity, significant endemism, and continuing deforestation, Myers et al. (1999) designated the Atlantic Forest as a biodiversity hotspot.

Forty-four (Thomas et al. 1998) to fifty-three percent (Mori et al. 1981) of the tree species and 49.5% of the seed plants (Zappi et al. 2015) of the Atlantic Forest may be endemic. For Lecythidaceae species in the Atlantic Forest, Smith et al. (2016) calculated that 50% of the species are endemic and threatened with extinction. The presence of only *Gustavia augusta* out of the 42 species of *Gustavia* (Map 8) as well as the total absence of the actinomorphic-flowered species of *Allantoma* (Map 10) and *Grias* (Map 7) in the Atlantic Forest demonstrates that actinomorphic-flowered species did not diversify in eastern Brazil.

Asymmetric distribution (i.e., high diversity in Amazonia and low diversity in the Atlantic Forest) also occurs in other clades of Lecythidaceae. *Eschweilera ovata* is the only species of the *E. parvifolia* clade in the Atlantic Forest, which has over 65 species in South and Central America. Another clade with a similar distribution is the *L. poiteaui* (Map 15) clade. The asymmetric distributions of these clades suggest that they migrated into the Atlantic Forest via a northern route from Amazonia during a time when the dry thorn scrub forest and savanna were covered by more humid forests (Costa 2003). The *L. pisonis* clade (Map 13) has equal numbers in the Atlantic Forest as it does outside this area.

Another hypothesis is that species of Lecythidaceae could have migrated stepwise along higher, wetter areas (called *brejos*) from Amazonia into the Atlantic Forest (Andrade-Lima 1977), or *vice versa*. This suggestion seems unlikely because it would have been difficult for seeds from at least two trees to disperse from one *brejo* to another and arrive in close enough proximity to cross-pollinate. Individual trees would infrequently produce seeds because of the low survival rate of self-pollination in Lecythidaceae (Moritz 1984).

Eschweilera nana of the *E. tetrapetala* clade is a widespread savanna species of planalto of central Brazil (Map 20) that shares morphologically distinct characters with six Atlantic Forest endemics. Huang et al. (2015) retrieved *Eschweilera nana* as sister to *E. tetrapetala* and *E. alvimii*, which are morphologically similar to four species not included in the molecular analysis (*E. complanata* S.A. Mori, *E. compressa* [Vellozo] Miers, *E. mattos-silvae* S.A. Mori, and *E. sphaerocarpa* M. Ribeiro et al, [Ribeiro et al. 2016]).

The species of the *tetrapetala* clade differ from the *Eschweilera integrifolia* and *E. parvifolia* clades in the following features: presence of a single-coiled vs. at least a double-coiled androecial hood; the lack of vestigial stamen nectaries vs. the presence of vestigial stamen nectaries; more than a single row vs. a single row of ovules in each locule; seed coats with impressed primary veins vs. seed coats without impressed primary veins; seeds with higher order veins not showing between the primary veins vs. higher order veins showing between the primary veins; and a basal instead of a lateral or spreading aril. The *E. tetrapetala* clade is the only clade confined to the Atlantic Forest and adjacent Brazilian savannas.

The migratory route of species into or out of the Atlantic Forest from southwestern Amazonia is located at the level of the states of Rio de Janeiro/Espírito Santo/southern Bahia. One example is the disjunct distribution between southwestern Amazonia and the Atlantic Forest of *Couratari macrosperma* (Map 25). The two populations appear morphologically similar but might represent two closely related species. In addition, there are three other Atlantic Forest endemics of the *Couratari* clade (*C. asterotricha*, *C. asterophora*, and *C. pyramidata* that belong to *Couratari* sect. *echinata* as defined by Prance (Mori & Prance 1990). We hypothesize that *C. macrosperma*

originally consisted of a large population that extended from southwestern Amazonia to the Atlantic Forest and was then isolated by the expansion of dryer vegetation thereby leaving one population in southwestern Amazonia and another in the Atlantic Forest. After the split the ancestor of *C. macrosperma* split into four lineages in eastern Brazil, a somewhat modified *C. macrosperma* and the morphologically distinct *C. asterotricha*, *C. asterophora*, and *C. pyramidata*. Other possibilities are that *C. macrosperma*, which is able to grow in both forest and disturbed habitats (Mori, Smith & Ribeiro, pers. obs.), may have moved from southwestern Amazonia to the Atlantic Forest or by migrating along gallery forests from Amazonia to the Atlantic Forest.

Cariniana estrellensis and *C. ianeirensis* have disjunct distributions between southwestern Amazonia and the central and southern parts of the Atlantic Forest (Maps 11, 25). The ability of species like *C. estrellensis* to migrate along gallery forests (Leite 2001) facilitates crossing savanna barriers. In contrast, *C. legalis* is restricted to the Atlantic Forest from Paraíba to Rio de Janeiro and from there arches inward in the state of São Paulo. The overall distribution of this species forms a "J" shape (Map 11). *Cariniana ianeirensis* ranges from southern Bahia to Rio de Janeiro and occurs disjunct in NW Bolivia and adjacent Mato Grosso. *Cariniana parvifolia* is endemic to the Atlantic Forest with a very limited distribution in northern Espírito Santo and southern Bahia.

In summary, compared to Amazonian Lecythidaceae, the Atlantic Forest has few species and all but one species (*Gustavia augusta*) have zygomorphic flowers. We conclude that Lecythidaceae migrated into the area when the dry areas between it and Amazonia were occupied by wetter forest. Once there new species, especially in the *Eschweilera tetrapetala* and *Couratari* clades, evolved. Today, 50% of the species of Lecythidaceae are endemic to the Atlantic Forest (Smith et al., 2016).

Evolution of floral zygomorphy in New World Lecythidacdeae

There are striking differences in androecial symmetry (Figs. 5–6) within the Lecythidaceae clade *sensu lato*. In the Old World, the Napoleonaeaceae (Map 2), Scytopetalaceae (Map 3), Lecythidaceae subfam. Foetidioideae (Map 4), and Lecythidaceae subfam. Barringtonioideae (Map 5) possess actinomorphic flowers. In contrast, the New World Lecythidaceae subfam. Lecythidoideae (Map 6) have three major types of androecial symmetry. *Allantoma*, *Grias*, and *Gustavia* have actinomorphic flowers (Fig. 5A) while the other genera have two types of zygomorphic flowers—one limited to the obliquely zygomorphic flowers of *Cariniana* (Fig. 5C) and the other includes zygomorphic genera with an androecial extension (= ligule) arising from a staminal ring (Fig. 5D, 6). Tsou and Mori (2007) have shown that the one-sided extension of a staminal tube (as in *Cariniana*) or from a staminal ring (all other species of zygomorphic-flowered Lecythidaceae) occurs on the abaxial side of the flower and suggest that this is caused by auxins stimulating growth on that side. There is one known example of a reversal from a zygomorphic to an actinomorphic androecium in *Corythophora rimosa* subsp. *rimosa* showing that changes in floral symmetry sometimes occur (N.P. Smith, pers. comm. 2015). Huang et al. (2015) and Mori et al. (2015) illustrate the floral features of all clades of New World Lecythidaceae.

Because no zygomorphic-flowered species occur in the Old World we assume that zygomorphy evolved in the New World from actinomorphic-flowered ancestors similar to species of subfam. *Barringtonioideae*. As mentioned above, species of barringtonioids have a broad staminal tube with many stamens arising from the rim thereby causing the androecium to resemble species of *Gustavia*; however, species of *Grias* share more morphological features in common with species of the subfam. *Barringtonioideae* (see "Worldwide distribution").

Once in the New World, floral zygomorphy of Lecythidaceae most likely evolved in response to pollination by bees. However, two New World Lecythidaceae, *Lecythis poiteaui* (Mori et al. 1978) and *L. barnebyi* (Mori & Prance 1990) are documented as bat-pollinated and, based on floral aromas, *Grias peruviana* may be pollinated by beetles because it possesses floral compounds similar to those

found in other plants pollinated by them (Knudsen & Mori 1996). New World Lecythidaceae offer fertile pollen, sterile pollen, and nectar as pollinator rewards (Mori et al. 1987).

Species of *Gustavia* have the least complex flowers in the New World and are visited by the greatest diversity of bees (Huang 2010). Species of this genus have poricidal anthers (not found in other species of New World Lecythidaceae) and, thus, are most efficiently pollinated by buzz-pollinating bees. Other bees, such as species of trigonids, are pollen robbers that are not efficient pollinators because they fill their pollen baskets and return directly to their nest without visiting other flowers (Mori & Boeke 1987; Potascheff et al. 2013). However, more robust trigonid bees are known to be pollinators of Lecythidaceae (Mori & Boeke, 1987). (Pollinators have not been recorded for *Allantoma* but the staminal tube suggests that nectar accumulates in the tube and serves as a reward to attract pollinators. The faintly scented flowers of *Cariniana estrellensis* open before dawn and pollinator visitation intensifies one hour after sunrise (Leite 2007). The nectar reward and aroma of this species most likely attracts relatively small bee pollinators.

Huang (2010) suggested that selection for pollination by large bees is the key to understanding the evolution of zygomorphic flowers in New World Lecythidaceae. She found that individuals of large-bodied species of *Xylocopa* (carpenter bees) visit both actinomorphic and zygomorphic flowers and hypothesized that species similar to this genus were the initial drivers of evolution of zygomorphic flowers in Lecythidaceae. Subsequently, long-tongued euglossine bees (Mori & Boeke 1987) also became important pollinators of New World Lecythidaceae.

Morphological adaptations present in at least some New World Lecythidaceae with staminal ring, zygomorphic flowers are the: (1) petals that press against the androecium to block entry into the flower by pollen and nectar robbers; (2) closure of the androecial hood opening against the staminal ring to stop entry into the flower by nectar and pollen robbers (Fig. 5D); (3) yellow honey guide spots at the entrance into the androecium; (4) formation of coiled androecial hoods (Fig. 6I–J, 6L–M) to limit nectar removal to bees with long proboscises; (5) change from fertile stamens (Fig. 6C) to staminodes (Fig. 6B) that provide sterile pollen for bees to feed their larvae; (6) yellow color of antherodes to direct bees to sterile pollen rewards; (7) change from fertile stamens to vestigial stamen nectaries (Fig. 6J) that provide nectar; (8) an obliquely oriented style that places the stigma in a position that receives pollen from pollinator before new pollen is collected, and (9) the formation of an external flap (Fig. 6M) in the *Couratari* clade. The *Couratari* flap overlaps the androecial hood and, thus, provides another layer that robber bees have to drill through to gather nectar. Evidence for this is that androecial hoods of species of *Couratari* are seldom perforated by trigonid bees, whereas the hoods of other groups, such as the *Eschweilera integrifolia* and *E. parvifolia* clades, are often perforated.

Huang (2011) pointed out that the evolution of the different zygomorphic flower types is more complex than originally proposed by Prance and Mori (1979), Mori et al. (1978), and Mori and Boeke (1987). According to Huang, the androecial types of New World Lecythidaceae do not provide clear examples of linear floral evolution; for example, Mori and Prance (1990) suggested that an ancestral *Cariniana* was the first step in the evolution of zygomorphy in New World Lecythidaceae. Based on current cladograms (Fig. 2A), the *Couroupita* clade is basal to all other zygomorphic-flowered genera as well as the actinomorphic-flowered species of the *Allantoma* clade, which in turn is sister to the *Cariniana* clade (Fig. 2A). It is more likely that the flowers of the *Cariniana* clade did not lead to more advanced zygomorphic flower innovations. In addition, the *Couratari* clade possesses the most complex flowers of New World Lecythidaceae but molecular trees do not support the hypothesis that this clade is evolutionarily most advanced.

The current distributions of the different floral symmetry types of New World Lecythidaceae await interpretation about where zygomorphic flowers evolved and how they migrated to different parts of the New World tropics. We hope that others will address the following questions:

(1) Did actinomorphic-flowered Old World Lecythidaceae colonize the New World? This hypothesis is based on the morphological similarity between *Grias* and *Gustavia* with the barringtonioids (see "Interchange between Old and New World Lecythidaceae"). The molecular data (Fig. 1) indicates that the relationship between *Grias* and *Gustavia* with the Barringtonoioideae is either plesiomorphic or homoplasious.

(2) Eastern Amazonia, the Guayana lowland biome, and the Atlantic Forest have relatively few actinomorphic-flowered species of Lecythidaceae (Map 26). Can we assume that these areas are not where actinomorphic-flowered species reached the New World.

(3) Species with small, membranous, tubular, zygomorphic androecia (also called tubular or obliquely zygomorphic, Fig. 5C) are found only in *Cariniana*. This genus is most diverse in southern Amazonia and has one *trans*-Andean species (*C. pyriformis*) found in eastern Panama near the boundary with Colombia, northwestern Colombia, and the Maracaibo Basin of Venezuela. There are no species in the Guayana lowlands and eastern Amazonia Brazil (Map 11). We propose that this type of androecium probably evolved from ancestors related to *Allantoma* (Fig. 5B) because of the similarity of the androecia in the two genera. However, *Cariniana* differs from *Allantoma* by its membranous *vs.* fleshy staminal tube and six instead of four or five petals. Are we justified in believing that the tubular zygomorphic androecium is an evolutionary dead end (Huang 2010), *i.e.*, it is not a precursor of more complex androecia as implied by Prance and Mori (1979)?

(4) Because zygomorphic-flowered Lecythidaceae only occur in the New World tropics, can we assume that this flower type evolved there?

(5) The variation of staminal ring zygomorphic flowers is greater in the Amazon than it is in any part of the New World. Of the 12 staminal ring zygomorphic clades (Figs. 1A–B), the following 11 clades are present in Amazonia: the *Couroupita* clade (Fig. 6A–B, 10B, Map 9), *Couratari* clade (Fig. 6M, 10F, Map 12), *Lecythis pisonis* clade (Fig. 6C, 10J, Map 13), *Bertholletia excelsa* clade (Figs. 6G, 10C, Map 16), *L. poiteaui* clade (Map 15), *L. chartacea* clade (Fig. 6H, Map 17), *Corythophora* clade (Fig. 6E, Map 18), *Eschweilera integrifolia* clade (Fig. 6L, Map 19), *E. tetrapetala* clade (Fig. 6K, 10I, Map 20), *L. corrugata* (Figs. 6D, 6F, Map 21), and *E. parvifolia* clade (Fig. 6I–6J, Map 22). The only clade outside of Amazonia with this type of androecium is the *Lecythis ollaria* clade (Map 14).   Did staminal ring zygomorphy first evolve in the Guayana lowlands and surrounding Amazonian lowlands?

(6) Several Amazonian clades with staminal ring zygomorphic flowers have one or two trans-Andean species that reach the other side of the Andes: *Couratari guianensis* (widespread) and *C. scottmorii* (*trans*-Andean endemic); *Couroupita nicaraguarensis* (*trans*-Andean endemic); *Lecythis ampla* Miers (*trans*-Andean endemic), *L. tuyrana* (*trans*-Andean endemic), *L. mesophylla* (*trans*-Andean endemic), and *L. corrugata* subsp. rosea (widespread). Did this flower type migrate from Amazonia into northwestern South America and eastern Central America?

CONCLUSIONS

Taxonomic changes

The three subfamilies of Lecythidaceae merit family status as the Foetidiaceae, Barringtoniaceae, and Lecythidaceae. These three clades are separated by differences in their distributions, morphology, and by the results of phylogenetic analyses (Fig. 1). The Napoleonaeaceae (Prance 2004) and the Scytopetalaceae (Appel 2004) are already recognized as separate families, but

the Angiosperm Phylogeny Group (Stevens 2004) still maintains five subfamilies in the Lecythidaceae.

We suggest that the *Eschweilera tetrapetala* clade (Fig. 2B) merits recognition as a separate genus based on its recovery as a highly supported clade based on molecular data and the possession of morphological features not found in the other two clades of *Eschweilera*. Michel Ribeiro, a doctoral candidate at the School of Tropical Botany of the Rio de Janeiro Botanical Garden, is studying this clade. The other two clades of *Eschweilera* (*E. integrifolia* and *E. parvifolia* clades) (Fig. 2B) have distinct morphological characters in common but the two clades are not retrieved as sister taxa based on molecular data (Huang et al. 2015) (Fig. 2B). We suggest that these two clades remain in *Eschweilera* until further information about their relationship is resolved. If the clades turn out to be sisters then they should be recognized as subgenera in order to show their close relationship as well as to avoid name changes. On the other hand, if they are not sisters they will have to be recognized as separate genera.

Two of the five clades of *Lecythis* have unique morphological characters and molecular data that set them apart from other clades of New World Lecythidaceae as defined by Mori and Prance (1990); thus, the *L. pisonis* and *L. corrugata* clades merit consideration as separate genera.

The *Lecythis ollaria/ L. poiteaui/ Bertholletia excelsa/ L. chartacea* clade (Fig. 2A) has <50% BS support and is difficult to differentiate by morphological features. If this clade is recognized as a single genus, then *Bertholletia excelsa* has to be transferred to *Lecythis* because the type, *L. ollaria*, was published earlier than other species in the clade (Dorr & Wiersema 2010a, 2010b).

Many species of *Eschweilera*, as currently circumscribed (Mori & Prance 1990) are difficult to distinguish. The first step in further study of this genus is to establish the relationship between the *E. integrifolia* and *E. parvifolia* clades as defined by Huang et al. (2015). If the separation of these clades is supported, the *E. integrifolia* clade should be recognized as a new genus and it should be monographed first because it has fewer species found in a more limited area (Map 19) than the *E. parvifolia* clade (Map 22).

Phytogeographic questions
In this study, we have described phytogeographic patterns of Lecythidaceae. Based on our observations, we suggest that future research addresses the following questions:

(1) How was the current tropical distribution of the Lecythidaceae clade *sensu lato* achieved (Map 1)?

(2) Is there a close relationship between the barringtonioids of the Old World and the actinomophic-flowered New World Lecythidaceae?

(3) How can the extreme disjunctions of (1) *Asteranthos brasiliensis* (Map 3) in the Amazon with other Scytopetalaceae in Africa and (2) *Petersianthus monocarpus* in Africa and *P. quadrialatus* in the Philippines be explained?

(4) Does the Pleistocene refuge theory play a major role in the diversification of New World Lecythidaceae?

(5) What impact did the uplift of the Andes have in the speciation and distribution of Lecythidaceae (Map 23)?

(6) What are the phylogenetic relationships between the *Eschweilera integrifolia* and *E. parvifolia* clades; e.g., did ancestral species of the *Eschweilera. parvifolia* clade give rise to the *E. integrifolia* clade?

(7) How did the appearance and disappearance of large bodies of water, such as lakes, wetlands, and sea embayments influence speciation of Lecythidaceae?

(8) Did species of Lecythidaceae migrate from both southeastern and southwestern Amazonia into the Atlantic Forest?

(9) Where did zygomorphic flowers evolve in the New World Lecythidaceae?

(10) Vicariance and long-distance dispersal are important drivers of speciation in Lecythidaceae but how are these events related to other drivers of speciation, e.g., pollination and dispersal?

Importance of conservation

Species of New World Lecythidaceae are ecologically dominant in many lowland primary forests, especially in the Amazon Basin (Steege et al. 2013). The more disturbed primary forests become the fewer species of Lecythidaceae they harbor. This and other associated tree families (e.g., Arecaceae, Burseraceae, Chrysobalanaceae, Fabaceae, Sapotaceae, etc.) form an Amazonian guild that provides ecosystem services upon which life on earth depends. Extinction of trees, like the death of "canaries in a coal mine," should warn humans that the negative impacts on the world's ecosystem services would continue to get worse if primary forests of all types are not more rigorously protected.

Over the last 20 years, deforestation of tropical forests has continued unabated. Over this period, human population has increased by 23% and economic growth has soared by 153% (Venter et al. 2016). Watson et al. (2016) calculate that 10% of the wilderness areas of the world have been lost during the last two decades, especially in South America where that figure is 30%. It is obvious, that the planet is already experiencing global warming; air, water, and soil pollution; crop failure; and increasing human conflicts over the use of natural resources.

Ferry Silk et al. (2015) estimated that there are at least 40,000 but perhaps as many as 53,000 tree species found in tropical forests. These authors compare tropical tree diversity with the 124 species of trees that grow in temperate Europe, demonstrating the overwhelming tree diversity of the tropics. In contrast, a study in Central Amazonian Brazil recorded 300 species of trees greater than 10 cm DBH in a plot of just 100 hectares (Oliveira & Mori 1998). In order to save tropical trees, the survival of plants and animals that depend upon them, and the ecosystem services they provide, it is essential to protect currently established biological reserves as well as continue to establish governmental, NGO, and private preserves as fast as possible. However, this strategy will not work unless human population and excessive consumption are also controlled!

that makes it possible to publish papers that might not be accepted in other journals because they are too long or because hypotheses are not tested. This is especially important for senior botanists because it allows them to leave a more complete legacy of what they have accomplished during their careers.

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ACKNOWLEDGEMENTS

TABLES

Table I.   The number of species in each of the subclades of the Lecythidaceae clade.   The clades correspond to those circumscribed by Huang et al. (2015) and Mori et al. (2015).   Note that Huang et al. (2015) recognize clades within *Eschweilera* and *Lecythis* that were previously delimited by Mori and Prance (1990) but these two genera are not monophyletic.   In order to determine the total number of species in *Eschweilera* fide Mori and Prance (1990) the species in the *Eschweilera parvifolia, E. integrifolia*, and *E. tetrapetala* clades need to be added together.   Likewise, the number of species in *Lecythis* fide Mori and Prance (1990) is the sum of the number of species in the *L. pisonis, L. ollaria, L. poiteaui, Bertholletia excelsa*, and *L. chartacea* clades.

Family	Subfamily	Genus/clade	Species	Distribution	References
Napoleonaeaceae					Kunth, 1939; Liben, 1971; Prance & Jongkind, 2015
		Napoleonaea clade	15–17	West & Central Africa	
		Crateranthos	04	West Africa	
Scytopetalaceae					Apple, 1996, 2004
	Scytopetaloideae				
		Scytopetalum clade	04	West Africa	
		Oubanguia clade	03	West Africa	
		Asteranthos clade	01	Central Amazonia	
	Rhaptopetaloideae				
		Rhaptopetalum clade	10	West Africa	
		Pierrina clade	01	West Africa	
		Brazzeia clade	03	West Africa	
Lecythidaceae					
	Foetidioideae			West Africa, Madagascar, and Mascarene islands	
		Foetidia clade	17	Madagascar and several species on islands around Madagascar, 1 in East Africa	Prance, 2008; Prance & Jongkind, 2015
	Barringtonioideae			Southeast Asia	
		Barringtonia clade	69	Southeast Asia	Prance, 2012
		Careya clade	04	Southeast Asia	Prance & Kartawinata, 2013
		Chydenanthus clade	01	Southeast Asia	Prance & Kartawinata, 2013

		Petersianthus clade	02	1 in Africa, 1 in Philippines	Prance & Jongkind, 2015
		Planchonia clade	06	Southeast Asia	Prance & Kartawinata, 2013
	Lecythidoideae			New World tropics	
		Allantoma clade	07		Huang et al., 2008
		Bertholletia clade	01		Mori & Prance, 1990
		Cariniana clade	09		Huang et al., 2008; Mori, 1995
		Corythophora clade	04		Mori & Prance, 1990
		Couratari clade	19		Mori & Prance, 1990
		Couroupita clade	03		Mori & Prance, 1990
		Eschweilera	three clades = 84 spp.		
		E. integrifolia clade	ca. 19		Huang et al., 2015
		E. parvifolia clade	ca. 58		Huang et al., 2015
		E. tetrapetala clade	07		Mori & Prance, 1990; Ribeiro & Smith (2016)
		Grias clade	12		Prance & Mori, 1979; Clark & Mori, 2000; Mori et al., 2010; Cornejo & Mori, 2011, 2012
		Gustavia clade	44		Prance & Mori, 1979; Mori & Cornejo, 2013
		Lecythis	total in 5 clades = 30		
		L. chartacea clade	ca. 11		Mori & Prance, 1990
		L. corrugata clade	05		Huang et al., 2015
		L. ollaria clade	03		Huang et al., 2015
		L. pisonis clade	05		Huang et al. 2015; Smith et al., 2012
		L. poiteaui clade	06		Huang et al., 2015; Smith et al., 2016

Table II. Lecythidaceae fossil record. Arranged in chronological order of publication.

Taxon	Organ	Age	Distribut.	Citation
Lecythis neriifolia	Leaves	Tertiary	Chile	Englehardt 1891
Couratari tertiaria	Leaves	Tertiary	Ecuador	Englehard 1895
Lecythidophyllum	Leaves	Miocene	Southern Mexico	Berry, 1923
Lecythidoanthus kugleri	Flower	Miocene	Trinidad	Berry 1924
Couroupita ovata	Leaves	Late Tertiary	Bahia, Brazil	Hollick & Berry, 1924
Lecythioxylon brasiliense	Wood	Cretaceous	Piauí, Brazil	Milanez, 1935
Couroupita santanderiensis	Leaves	Miocene	Santander, Colombia	Berry 1936
Barringtonioxlon deccanense	Wood	Upper Cretaceous to Early Eocene	India	Shallom 1960
Barringtonioxlon eopterocarpum	Wood	Upper Cretaceous to Early Eocene	India	Prakkash & Dayal 1965
Marginipollis coccinus	Pollen	Upper Tertiary	Nigeria	Clarke & Frederiksen 1968
Rostriapollenites kuchensis	Pollen	Eocene	India	Venkatachala & Kar 1968
Lecythidopyon girardotanum	Fruit	Not cited	Cundinamarca Colombia	Huertas 1969
Barringtonia sp.	Leaves	Eocene	Alaska	Wolfe 1972
Planchoniidites areolatoideus	Pollen	Tertiary	New Guinea	Khan 1976
Barringtonia sp.	Pollen	Lower Eocene	India	Muller 1981
Barringtonia assamicum	Wood	Oligocene	India	Agarwall et al. 2000
Barringtonia preracemos	Fruit	Tertiary	India	Mehrotra 2000
Carinianoxylon, brasiliense	Wood	Tertiary	Maranhão, Brazil	Selmeier 2003
Cariniana & Eschweilera	Wood	Middle Eocene	Pebas formation, Brazil	Pons & de Franceschi 2007
Barringtonia sp.	Pollen	Middle Eocene	Germany	Manchester et al. 2015
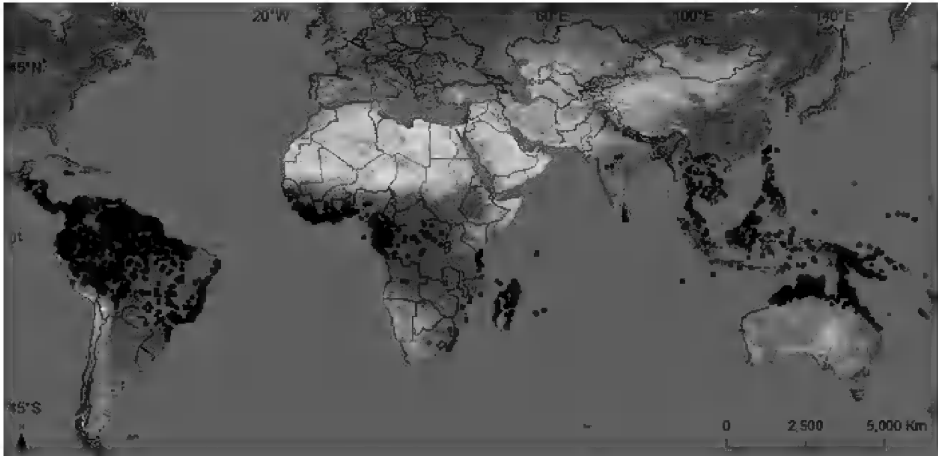
MAP 1.   The Lecythidaceae clade (including Napoleonaeaceae, Scytopetalaceae, Lecythidaceae subfam. Foetidioideae, Lecythidaceae subfam. Barringtonioideae, and Lecythidaceae subfam. Lecythidoideae) are native to Central and South America, Africa, and Asia.
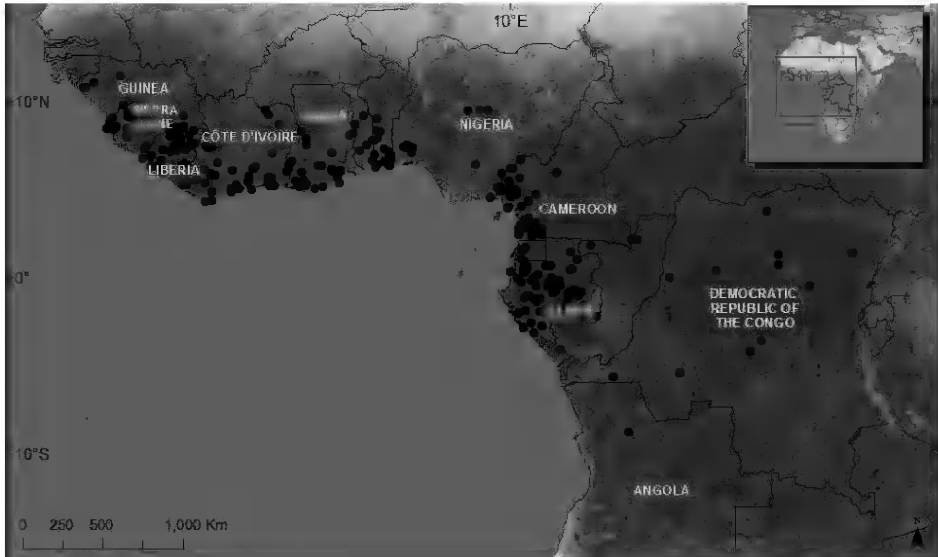
MAP 2.   Distribution of the Napoleonaeaceae.   This family is found only in western and central Africa.
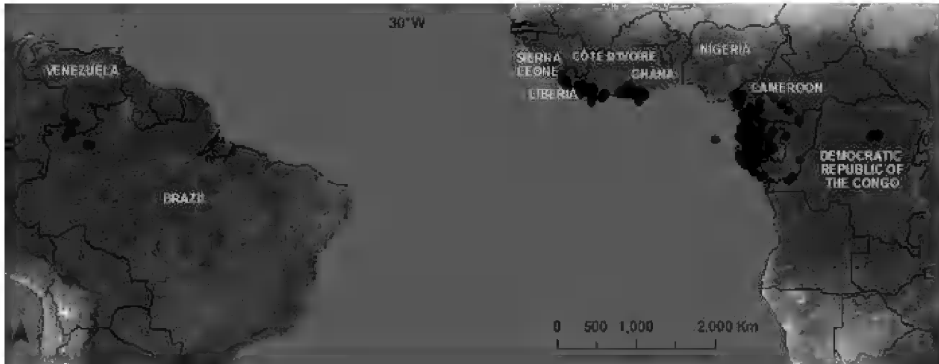
MAP 3. Distribution of Scytopetalaceae. This family is found in western and central Africa and one species, *Asteranthos brasiliensis*, is limited to northwestern Amazonian Brazil and adjacent Venezuela.
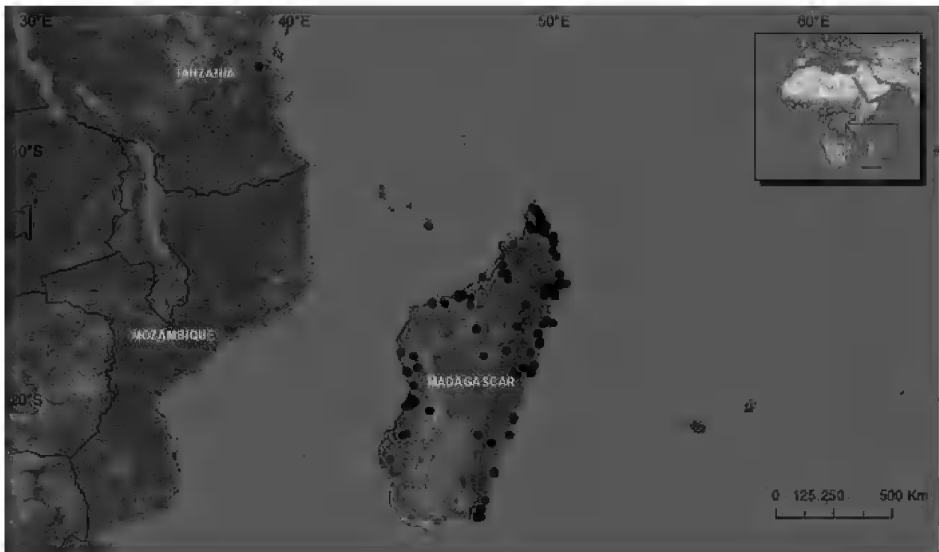
MAP 4. Distribution of Lecythidaceae subfam. Foetidioideae. This monogeneric subfamily is represented by 14 species in Madagascar, three species in the Mascarene Islands, and 1 species in western Africa (Prance, 2008).
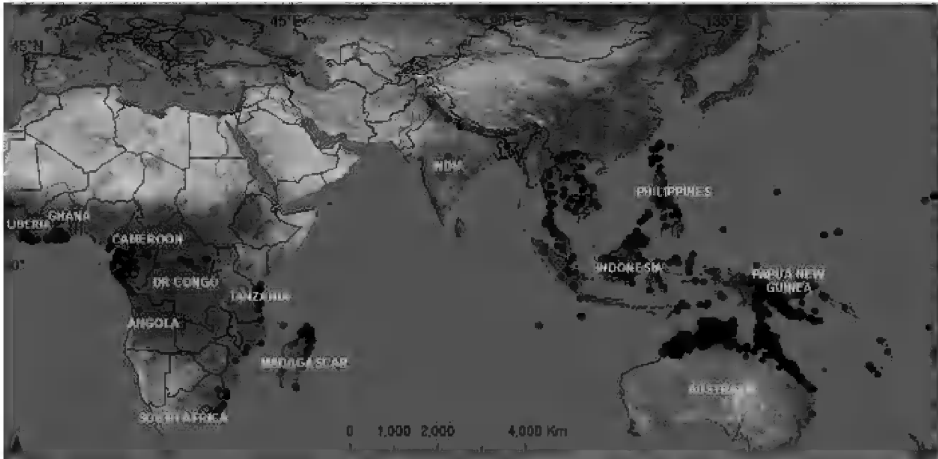
MAP 5.   Distribution of Lecythidaceae subfam. Barringtonioideae.   This subfamily is well represented in India, northern Australia, and southern Asia. In eastern Africa it is represented by two species (*Barringtonia asiatica* and *B. racemosa*), both of which have fruits that float. In addition, the common and widespread *Petersianthus macrocarpus* is the only species of subfam. Barringtonioideae that occurs in eastern and central Africa. The other species of *Petersianthus quadrialatus* is endemic to the Phillipines (Prance, 2012). There are no native barringtonioids in the New World and nearly all of the cultivated individuals are *Barringtonia asiatica*.
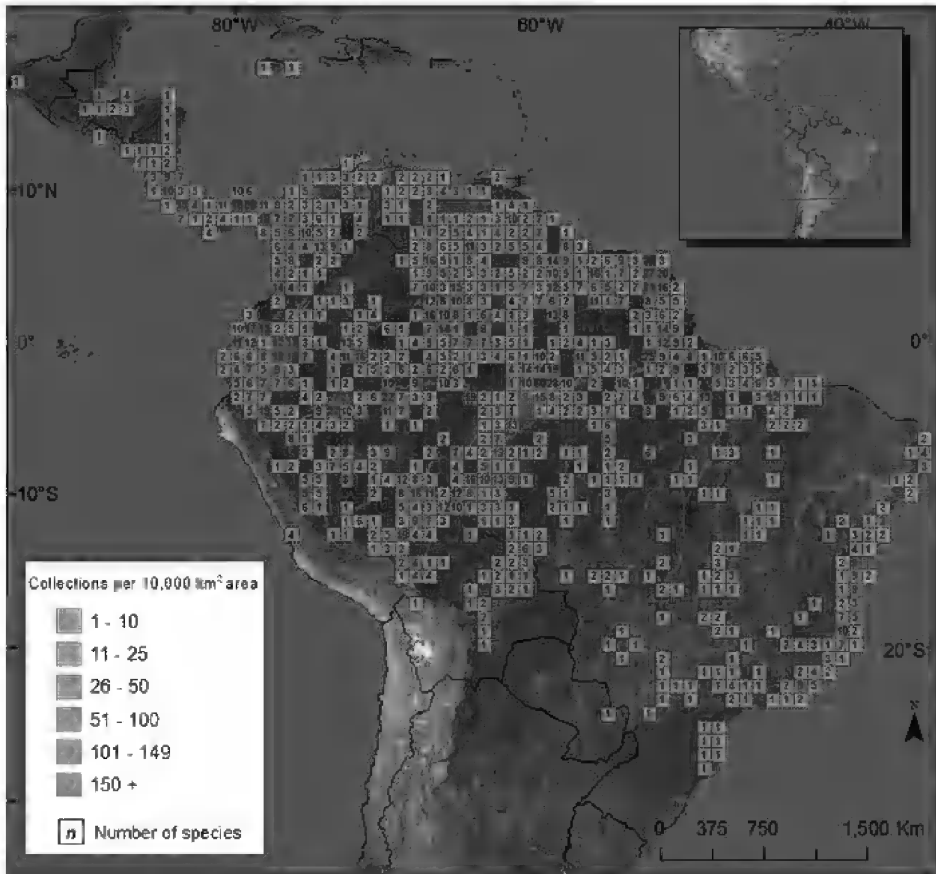
MAP 6. Distribution of Lecythidaceae subfam. Lecythidoideae. This subfamily is restricted to the New World tropics ranging from southern Brazil (*Cariniana estrellensis*) to Veracruz, Mexico (*Eschweilera mexicana*).
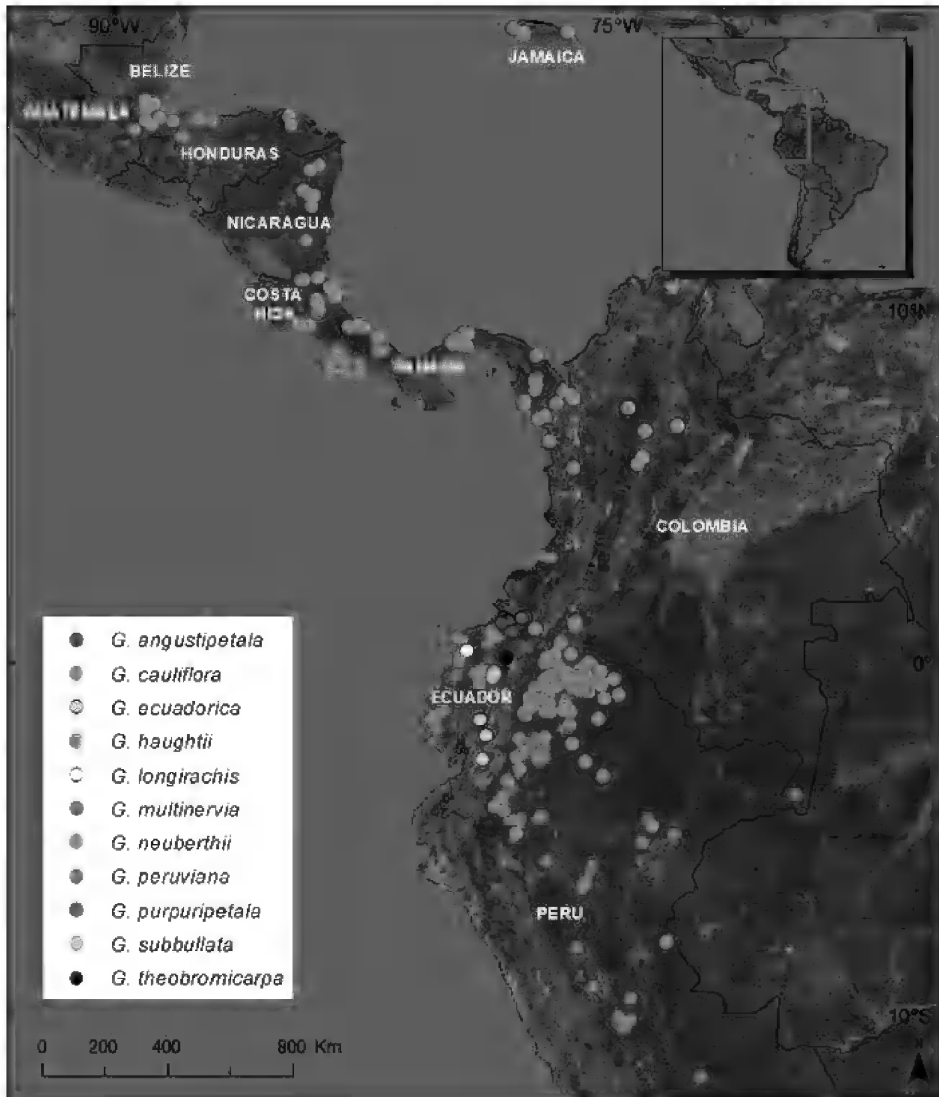
MAP 7. Distribution of the actinomorphic-flowered, monophyletic *Grias* clade. This genus is found mostly in the northwestern Andes but two species occur in western Amazonia (*G. neuberthii* and *G. peruviana*) and one species, the widespread *G. cauliflora*, is disjunct between Central America and Jamaica.
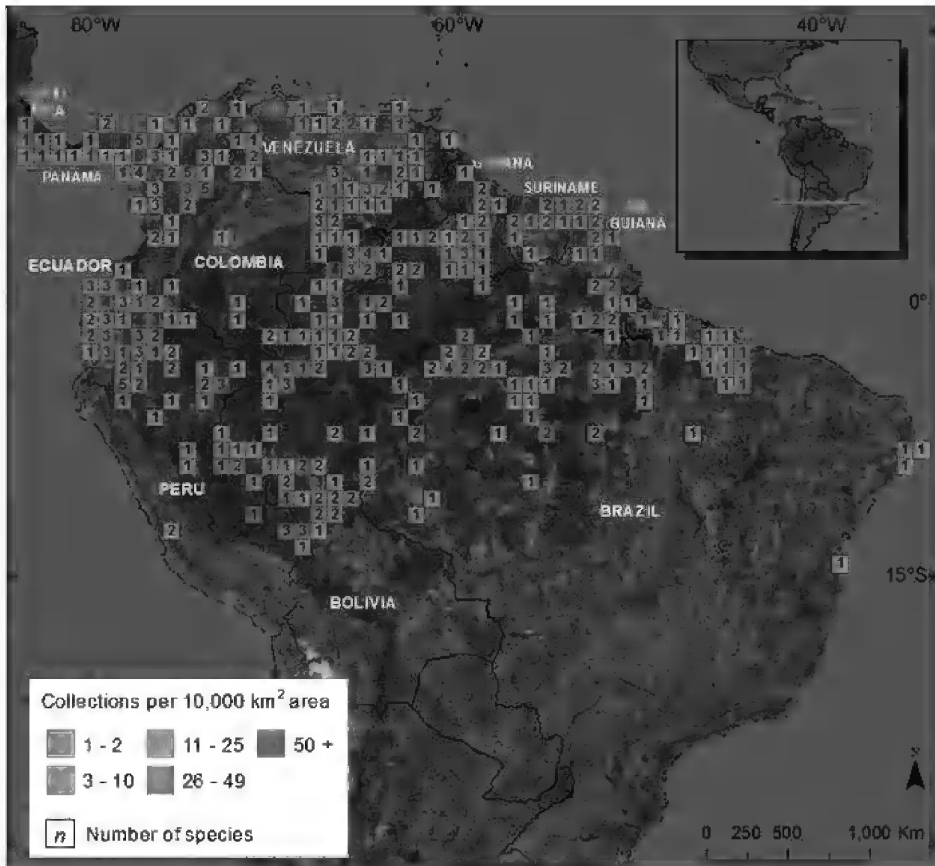
MAP 8.   Distribution of the actinomorphic-flowered, monophyletic *Gustavia* clade.   This genus occurs throughout most of the New World tropics.   However, only one species is found in the Atlantic Forest of Brazil and diversity is low throughout the Guianas and eastern Amazonian Brazil.   High diversity of this clade is found from eastern Panama to northwestern Ecuador.
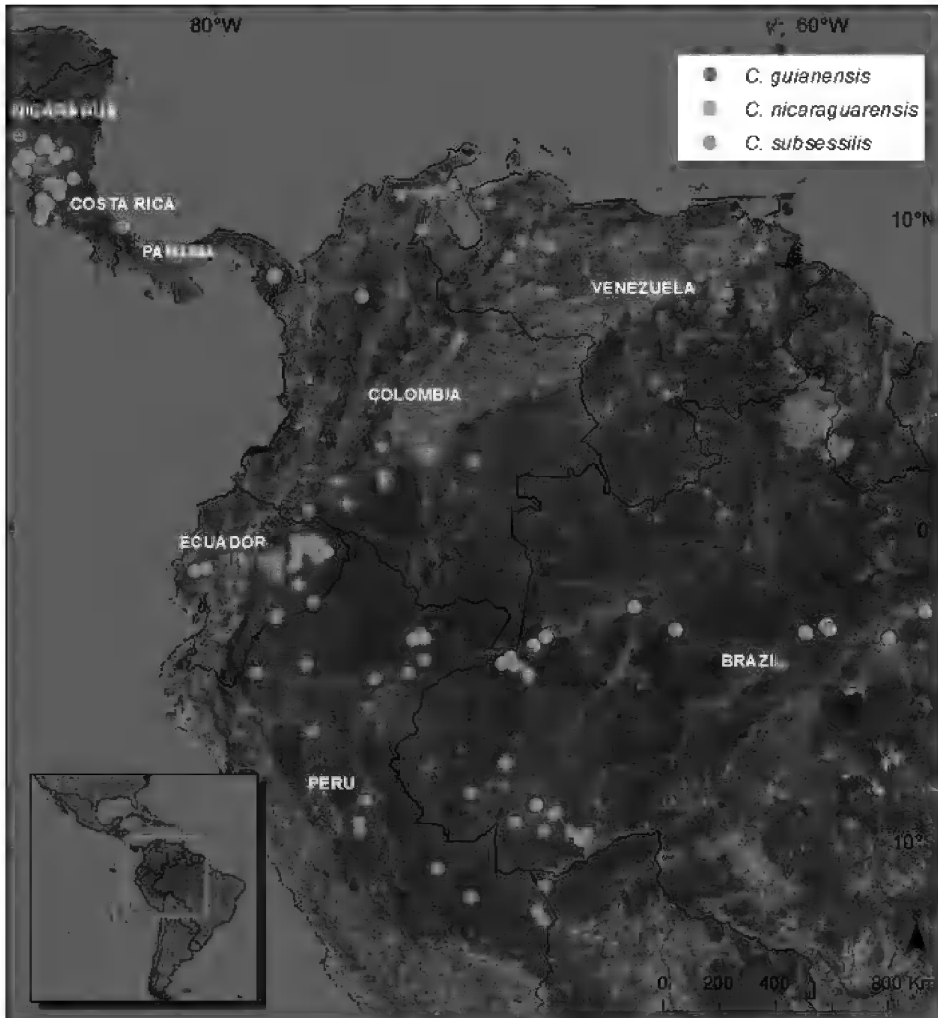
MAP 9. Distribution of the zygomorphic-flowered, monophyletic *Couroupita* clade. There are three species in this clade, two east of the Andes (*Couroupita guianensis* and *C. subsessilis*) and one west of the Andes (*C. nicaraguarensis*). Collections of cultivated species are not included on this map.
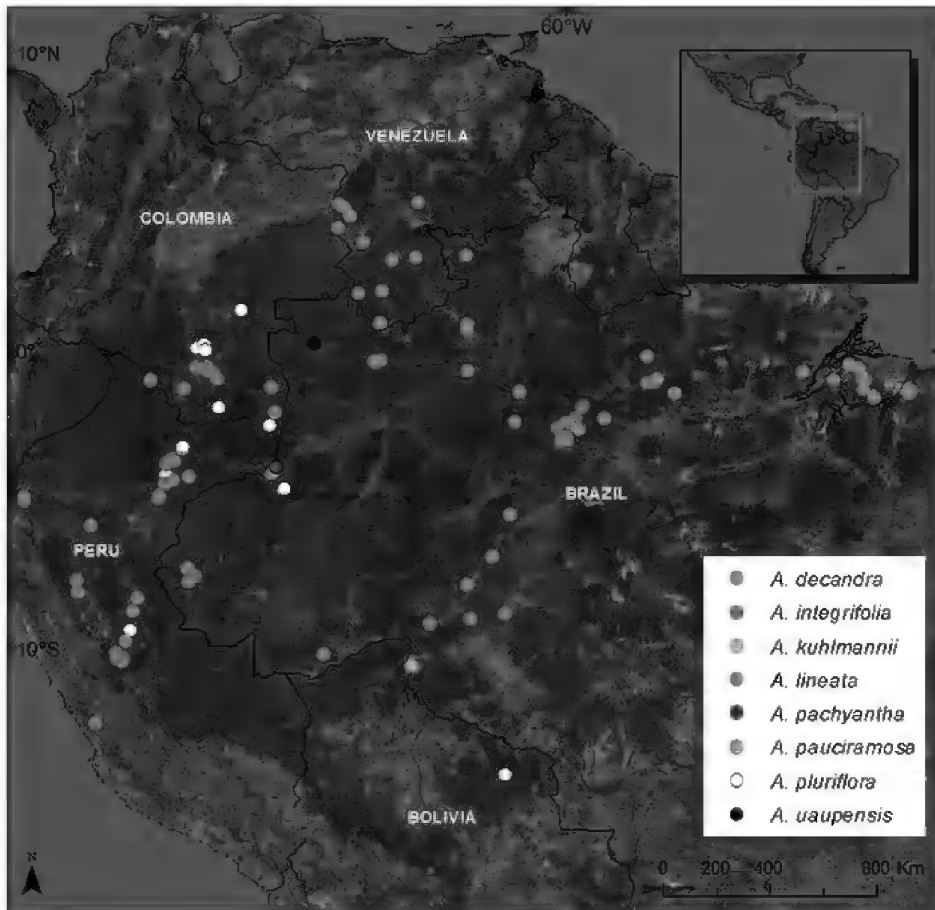
MAP 10. Distribution of the actinomorphic, monophyletic *Allantoma*. The greatest species diversity of this genus is in the northwestern Amazon. It is absent in the Guayana lowland flora, southeastern Amazonia, and the Atlantic Forest of Brazil. The disjunct collection from Bolivia is correctly identified as a species of *Allantoma* but the species has not been determined.
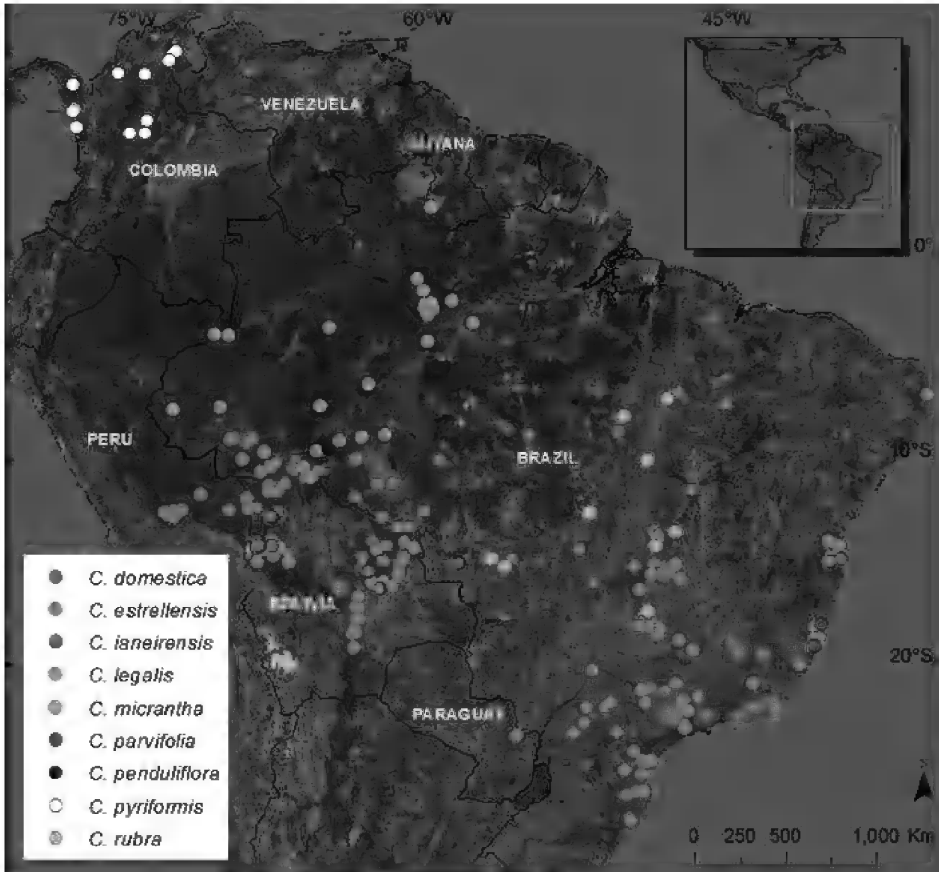
MAP 11. Distribution of the zygomorphic-flowered, monophyletic *Cariniana* clade. This genus is most speciose in a band from southwestern Amazonia to the Atlantic Forest of Brazil. Species of this clade are absent in eastern Amazonia, the Guayana lowlands, Venezuela, and Ecuador. *Cariniana pyriformis* occurs in northwestern Colombia, eastern Panama, and the Maracaibo Basin of Venezuela.
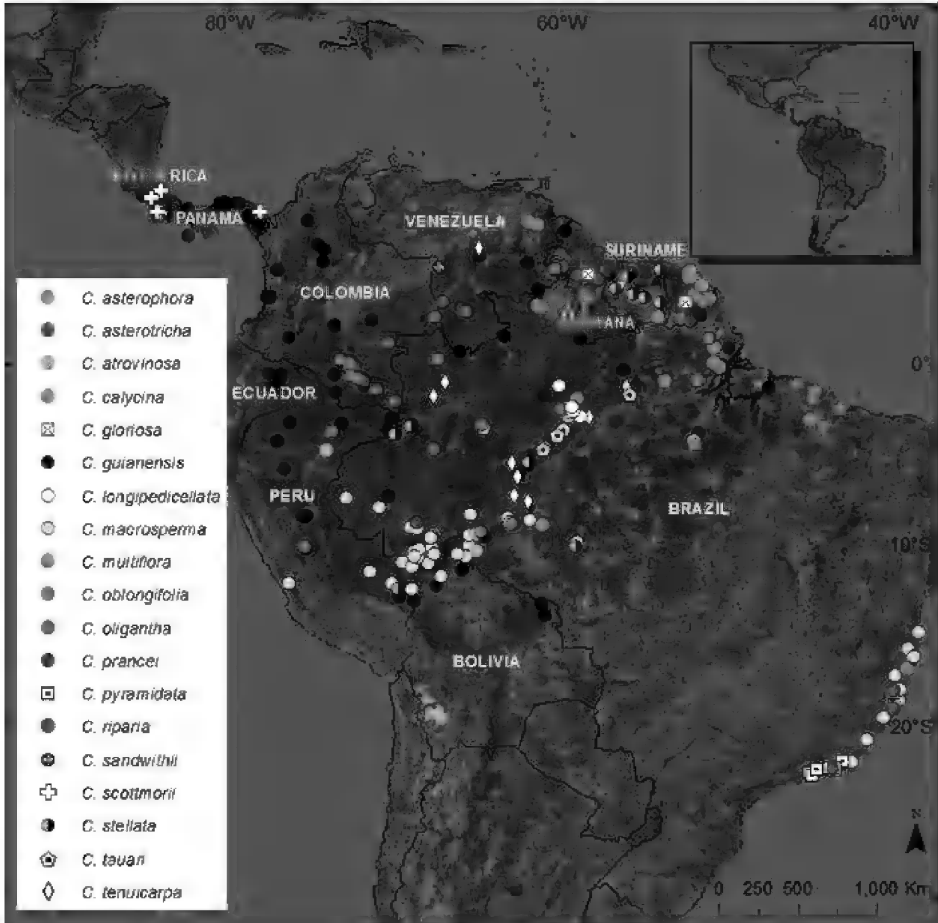
MAP 12. Distribution of the zygomorphic-flowered, monophyletic *Couratari* clade. Species of this clade appear in most lowland forests of the New World tropics but are usually absent from dryer areas. There is one trans-Andean species (*C. guianensis*), one Central America endemic (*C. scottmorii*), and four species in the Atlantic Forest of Brazil (*C. asterophora*, *C. asterotricha*, *C. macosperma*, and *C. pyramidata*).
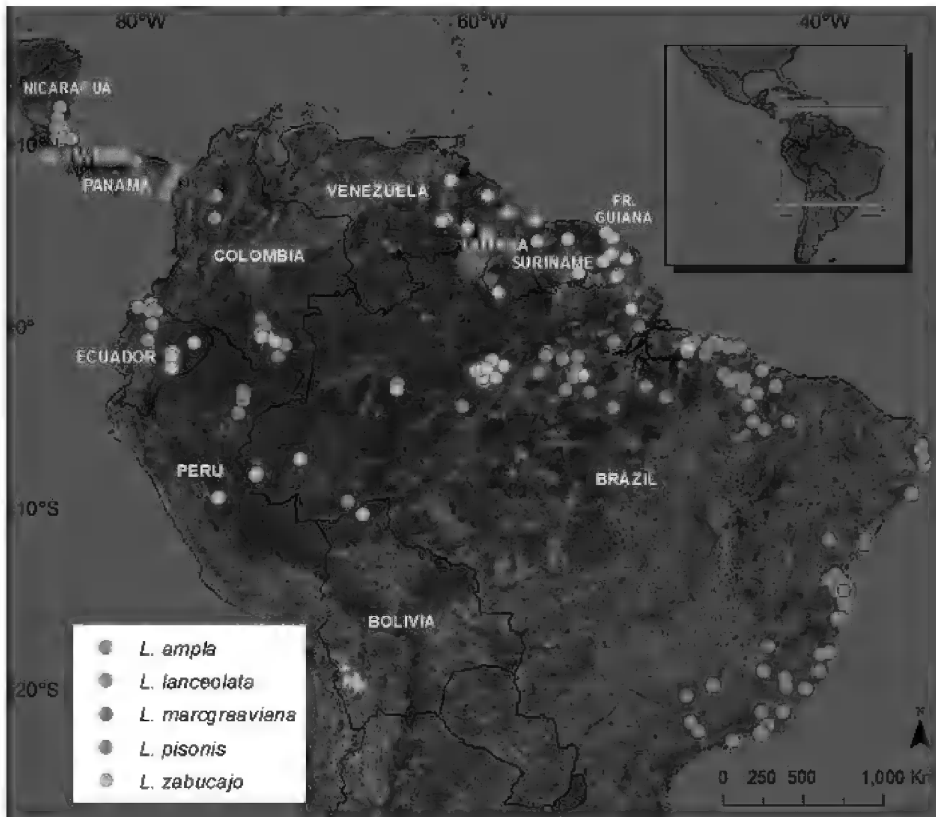
MAP 13. Distribution of the zygomorphic-flowered, monophyletic *Lecythis pisonis* clade (Huang et al., 2015). This clade is found in most of the lowland forests of lower Central America and South America but is usually absent from savanna, dry thorn scrub, and cloud forest vegetation types. *Lecythis pisonis* is cultivated so it is difficult to determine if some collections represent native plants.
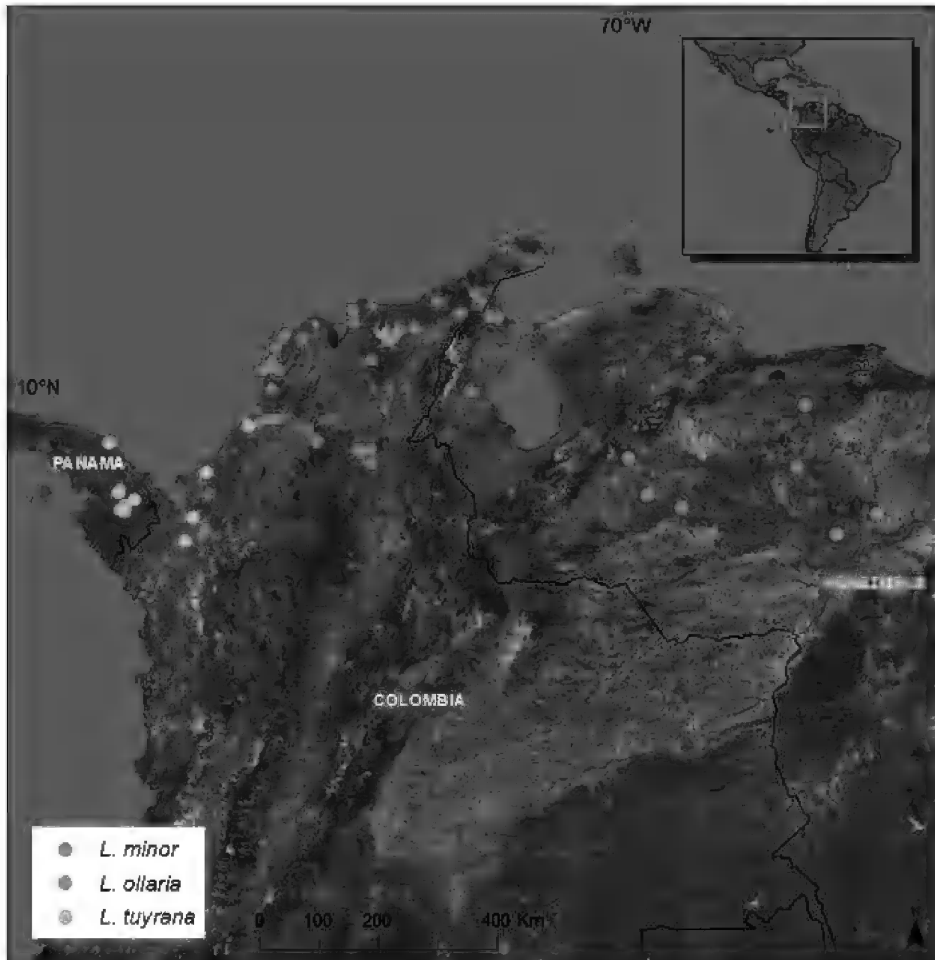
MAP 14. Distribution of the zygomorphic-flowered, non-monophyletic *Lecythis ollaria* clade (Huang et al., (2015). There are only three species in this clade: *Lecythis ollaria* (the type of *Lecythis*) found in savannas south of the Andes in Venezuela, *L. minor* in dry areas in northeastern Colombia, and *L. tuyrana* in lowland forests ranging from the Chocó of Panama into the Magdalena valley of Colombia.
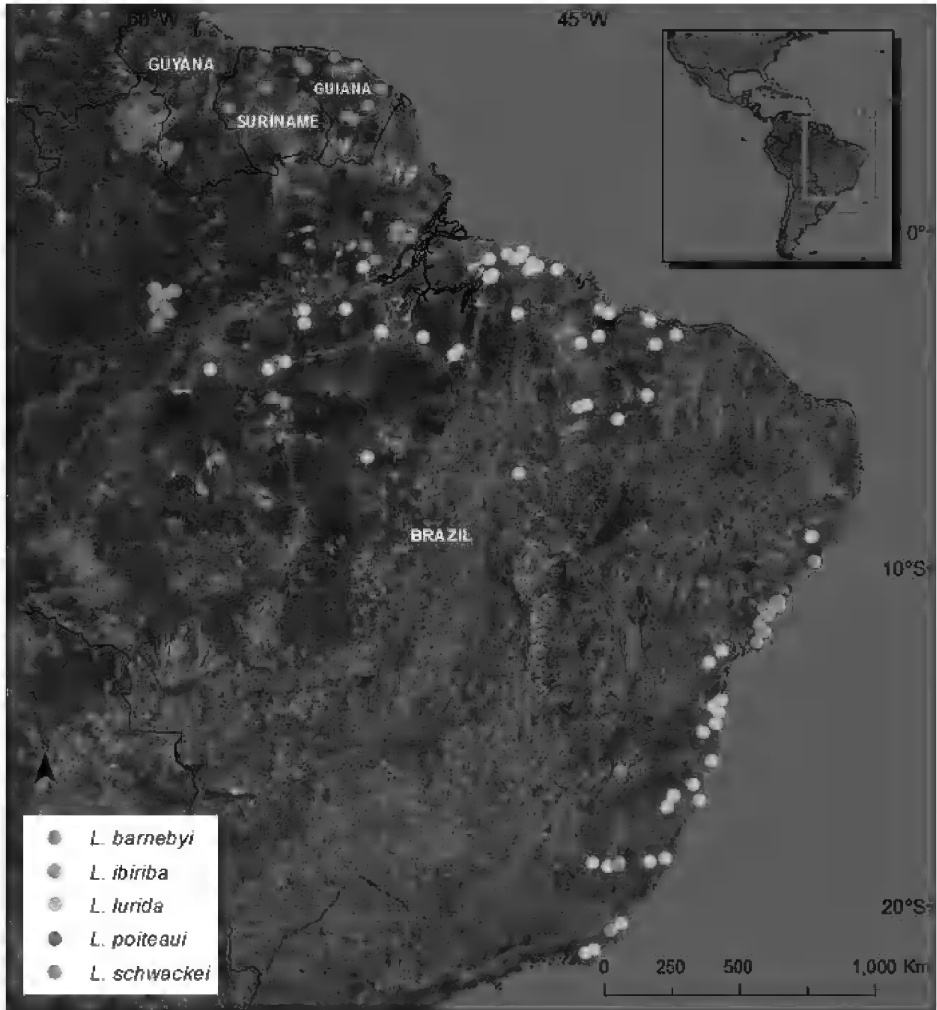
MAP 15. Distribution of the zygomorphic-flowered, non-monophyletic *Lecythis poiteaui* clade (Huang et al. 2015). This clade is found in the Guayana lowlands, central and eastern Amazonian Brazil, and the Atlantic Forests of Brazil. The Amazonian and Atlantic Forest species of this clade are currently separated by thorn scrub forest and savanna.
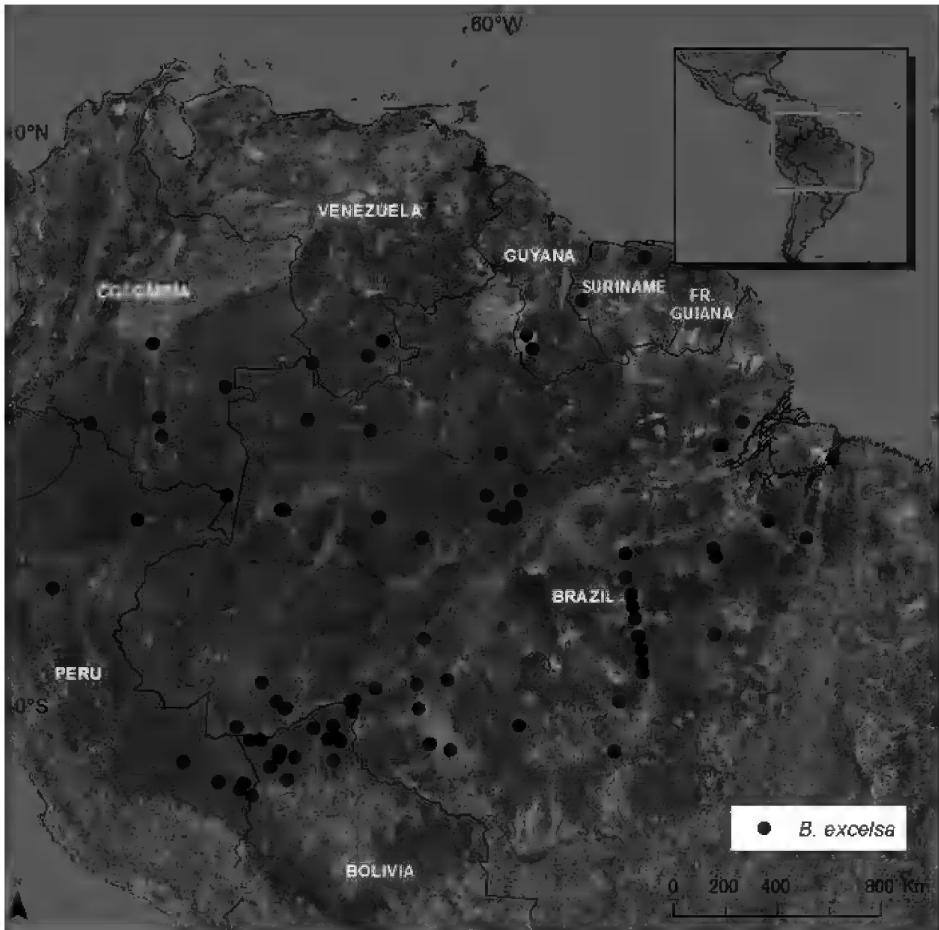
Map 16. Distribution of the zygomorphic-flowered, monotypic, non- phylogenetic *Bertholletia excelsa* clade. This clade is restricted to the Amazon Basin. Because of its edible seeds it has been carried from one region of the Amazon Basin to other parts of the Basin by humans; thus, the native distribution of this species is difficult to determine.
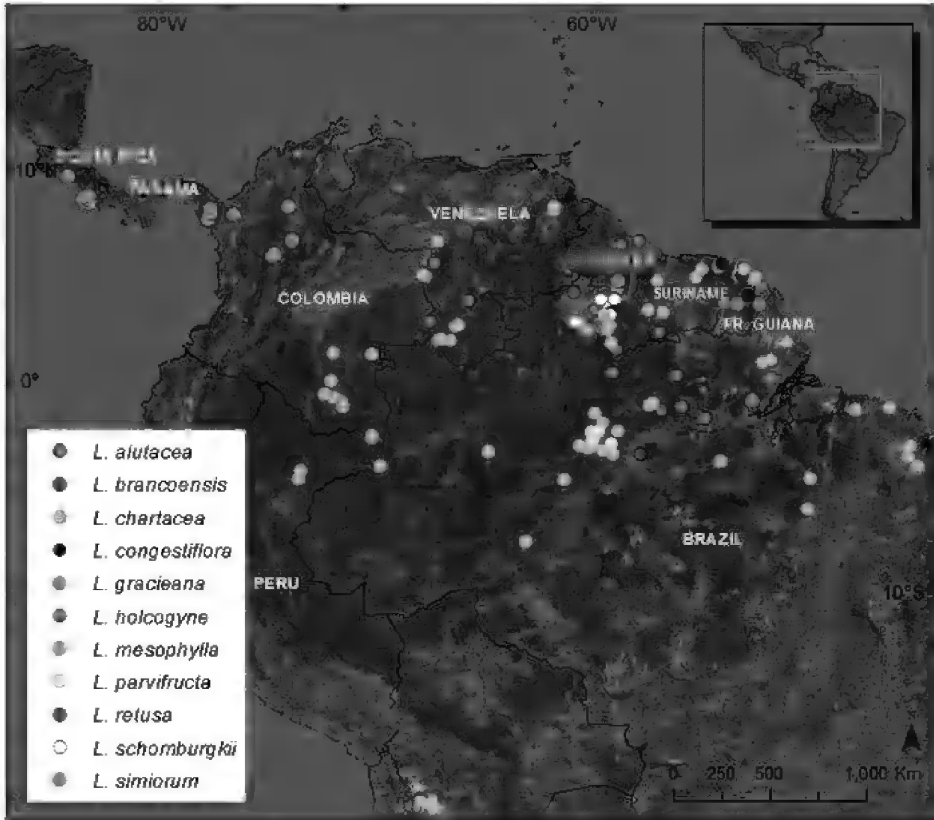
MAP 17. Distribution of the zygomorphic-flowered, non-monophyletic *Lecythis chartacea* clade. We now consider *Eschweilera congestiflora* and *E. simiorum* to be synonyms of *Lecythis congestiflora* Benoist and *L. simiorum* Benoist. This clade is distributed widely in Amazonia and is represented in eastern Panama and northwestern Colombia by *Lecythis mesophylla*. It is absent from the Atlantic Forest of Brazil.
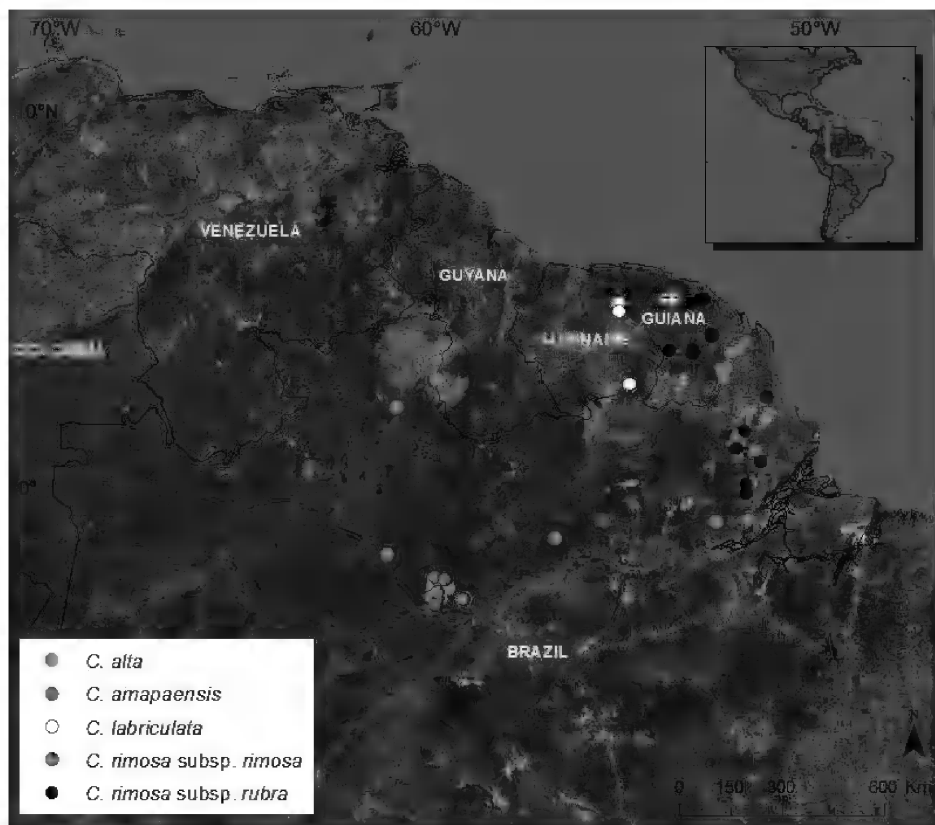
MAP 18. Distribution of the zygomorphic-flowered, monophyletic *Corythophora* clade. This clade is limited to the Guayana lowlands.
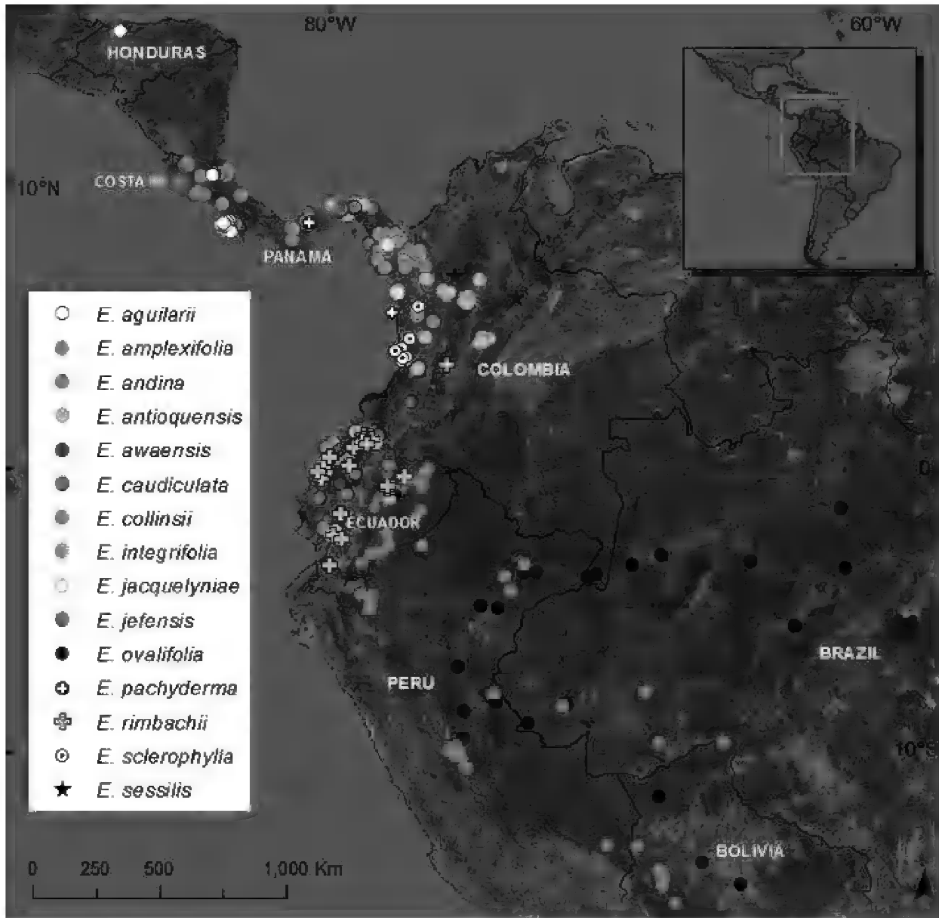
MAP 19. Distribution of the zygomorphic-flowered, non-phylogenetic *Eschweilera integrifolia* clade. This clade has two species found east of the Andes, the well-defined *E. ovalifolia* and *E. andina*, as well as numerous, poorly-defined species associated with the Andes into Central America as far north as Costa Rica.
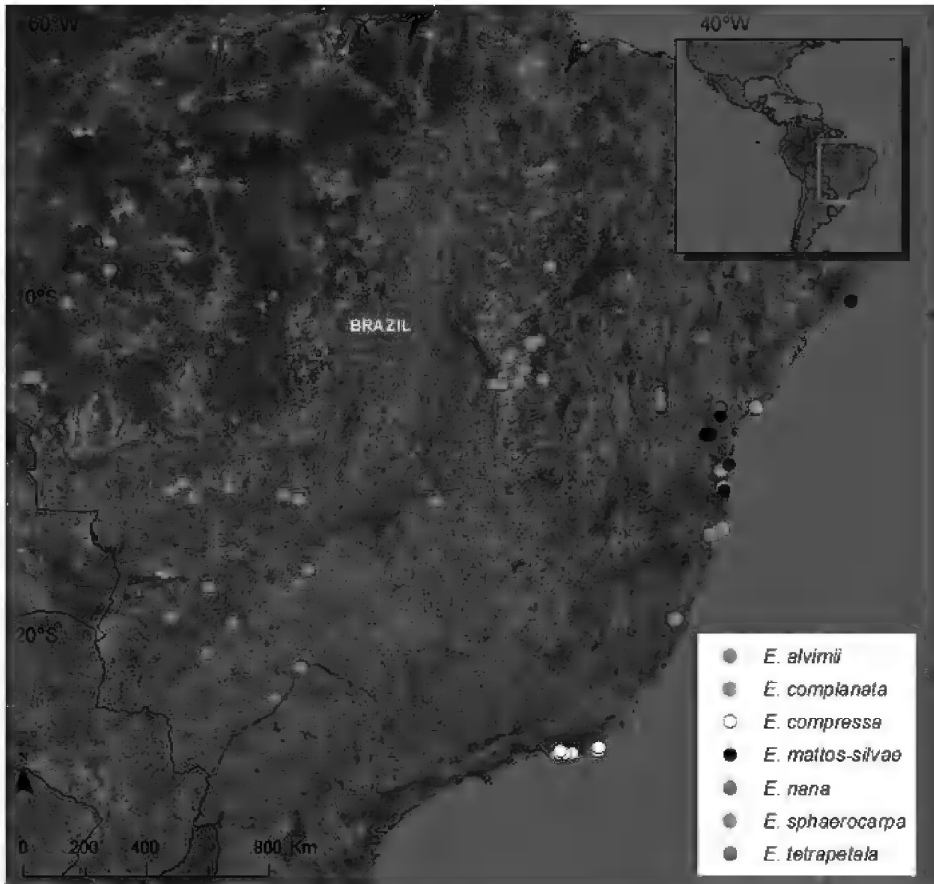
MAP 20.   Distribution of the zygomorphic-flowered, monophyletic *Eschweilera tetrapetala* clade. This clade has one widespread species in the savannas of central Brazil and six described species with limited distributions in the Atlantic Forest of eastern Brazil.
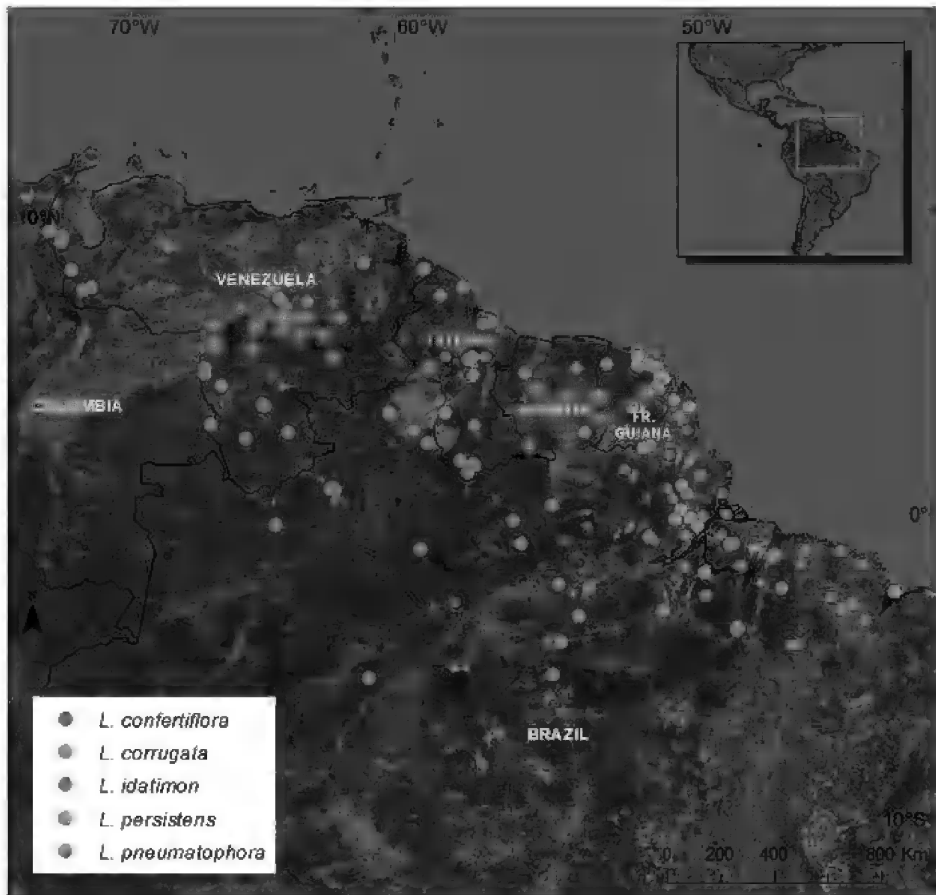
MAP 21. Distribution of the zygomorphic-flowered, non-monophyletic *Lecythis corrugata* clade. Species of this clade are mostly found in lowland Guayanan forests but some collections have been gathered south of the Amazon River.
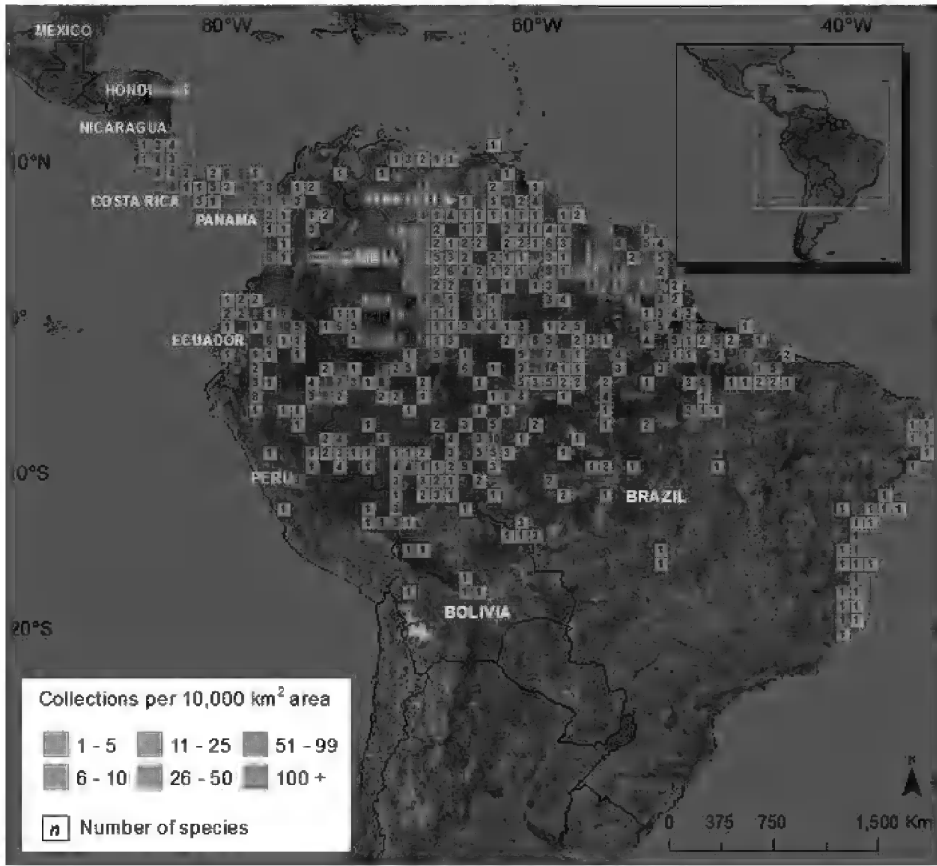
MAP 22. Distribution of the zygomorphic, non-monophyletic *E. parvifolia* clade. This clade is widely distributed throughout the Amazon, the Guayana lowlands, west of the Andes, and the Atlantic Forest where there is only one species of this species clade (*E. ovata*).
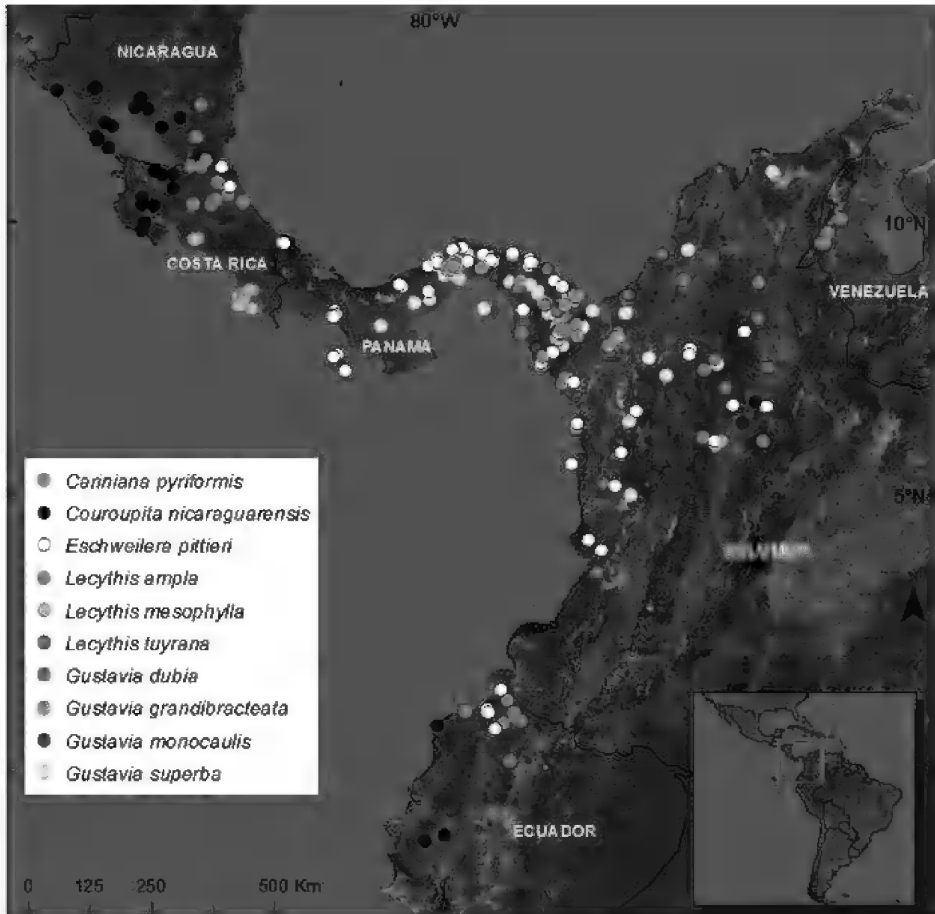
MAP 23. Distributions of selected species found in eastern Panama and northwestern South America. Such high diversity in this relatively small area appears to be promoted by the uplift of the Andes and the closing of the connection between North and South America.
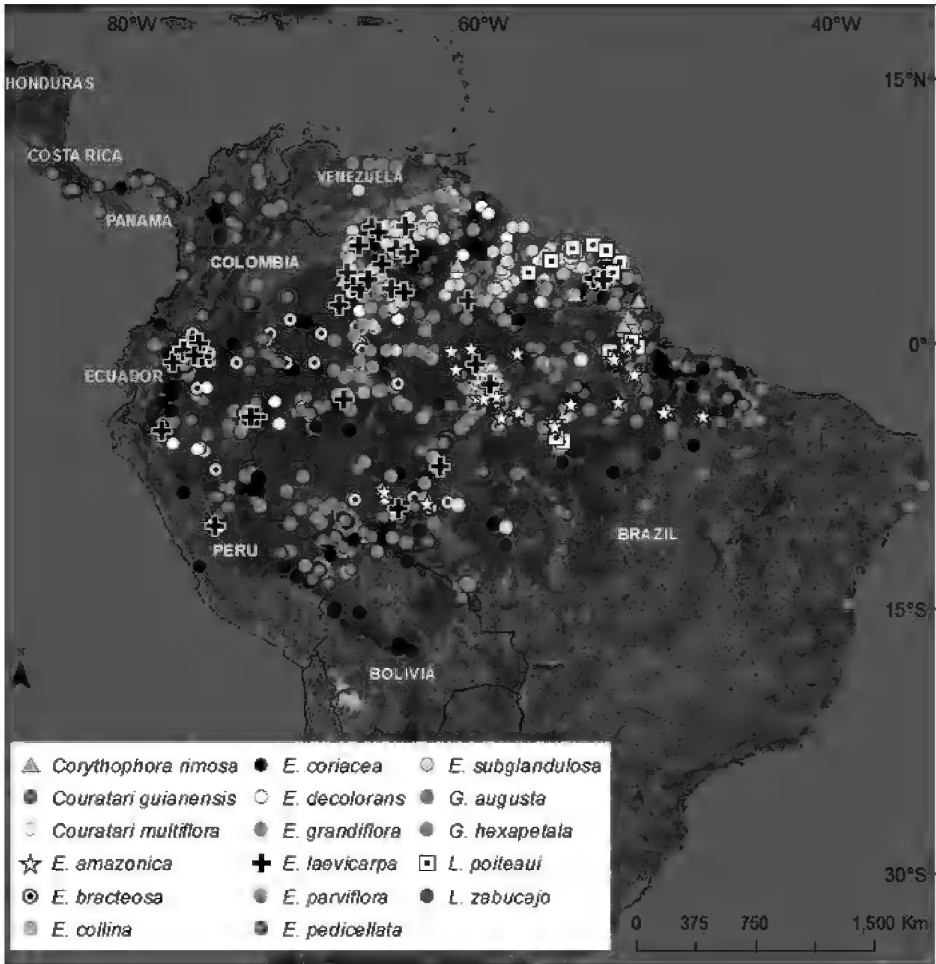
Map 24. Selected species of Lecythidaceae found in Central Amazonia. The diversity found in this area may have developed when lakes and oceanic intrusions receded and formed open habitats into which species of Lecythidaceae migrated from non-flooded areas such as the Guayanan lowlands (e.g., *L. barnebyi*, Map 15) and far western Amazonian (e.g., *E. tessmanii*. Map 19). In addition, other species may have been isolated on islands where they evolved *in situ* (e.g., *Lecythis barnebyi*).
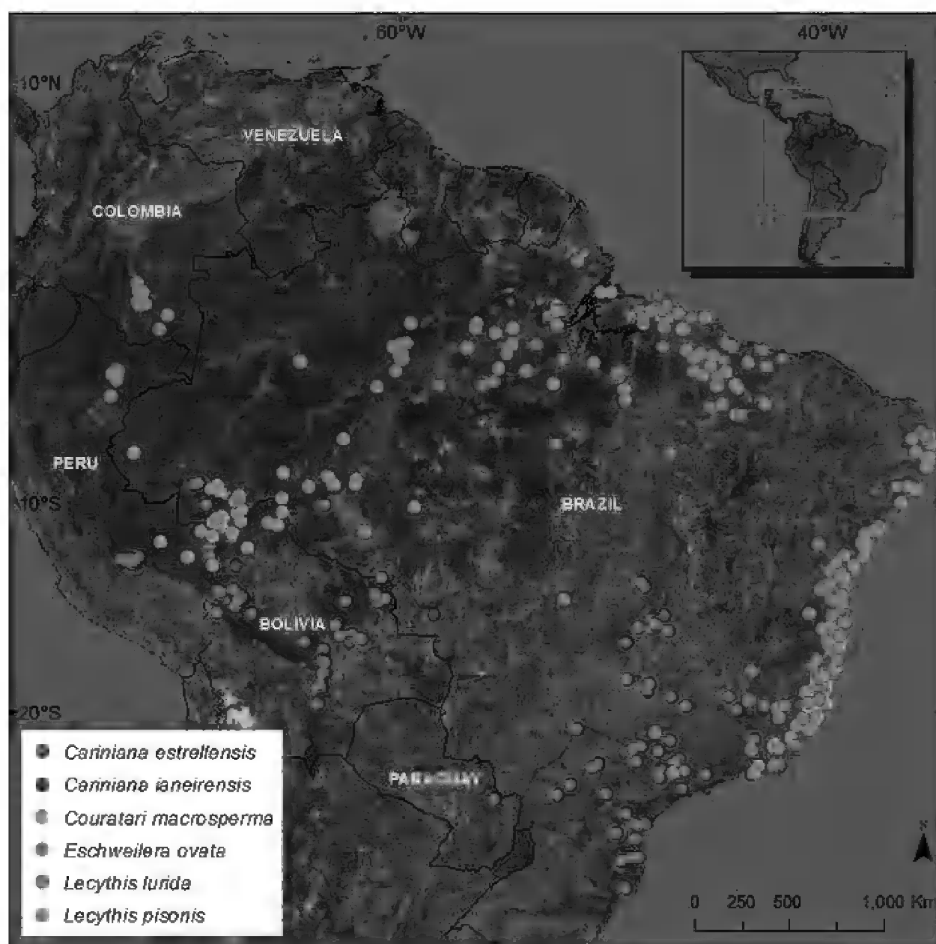
Map 25. Distributions of selected species of Lecythidaceae found in the Atlantic Forest of Brazil as well as in either the Planalto of Brazil, eastern Amazonia, or southwestern Amazonia.
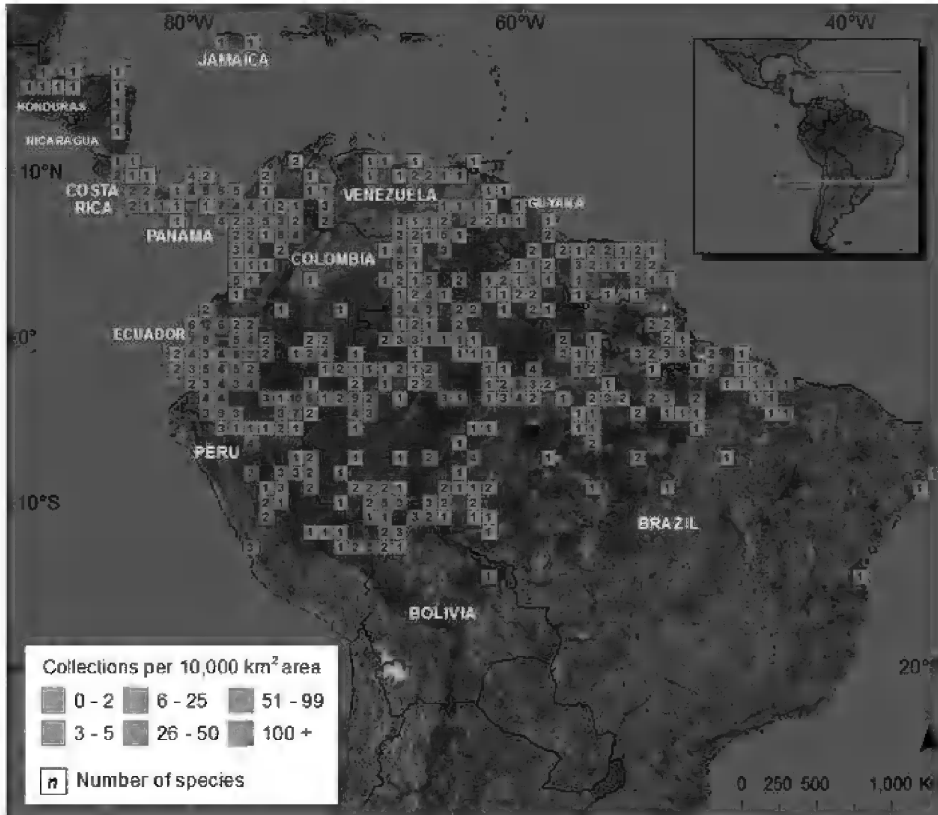
Map 26. Overall distributions of New World genera of Lecythidaceae with actinomorphic flowers (*Allantoma*, *Grias*, *Gustavia*). This map shows the colored coded collection density and the numbers indicate the number of species with this type of flower symmetry per degree grid square.
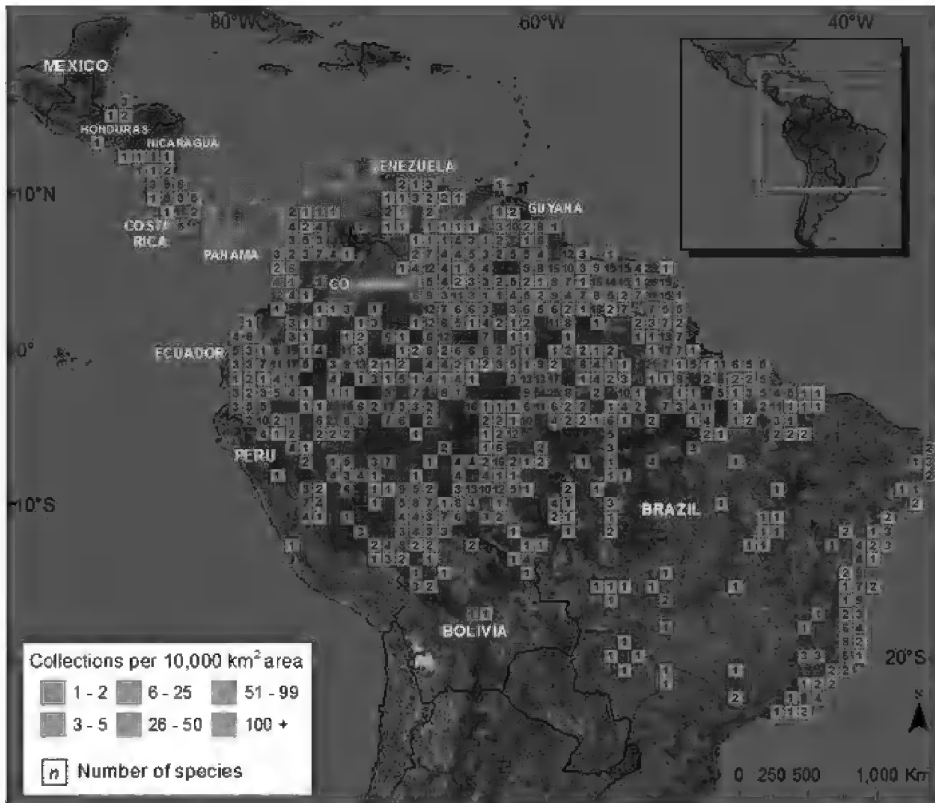
Map 27. Overall distribution of species with staminal ring zygomorphic flowers. Species of the following clades have this type of floral zygomorphy: *Bertholletia, Corythophora, Couratari, Couroupita, Eschweilera* (consists of three subclades and is not monophyletic), and *Lecythis* (consists of five subclades and is not monophyletic).

ARUM ITALICUM (ARACEAE) IS INVASIVE IN NEW YORK

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ABSTRACT
Spontaneous populations of *Arum italicum* (Italian Lords and Ladies) are documented from Bronx and New York counties in southeastern New York state. Three populations are documented from New York Co. (Manhattan): Inwood Hill Park with dozens of discrete clusters in an area of 2500 square meters of mostly spontaneous deciduous forest; Fort Tryon Park with dozens of discrete clusters in an area of 20,000 square meters of cultivated garden beds; and the Upper East Side of Manhattan, near Carl Schurz Park and the FDR Drive, with four discrete clusters in an area of about 60 square meters of open, highly disturbed, currently fallow ground. The Bronx Co. population, in the New York Botanical Garden, consists of two discrete clusters in an area of about 6 square meters of mostly native, deciduous forest. Each cluster consists of a few to dozens of plants. The Inwood, Fort Tryon, and NYBG populations are documented with herbarium specimens and DNA samples and the Carl Schurz population is documented by photographs in iNaturalist. Original observations on invasiveness, toxicity, control, management, and native alternatives are presented. The New York reports are new state records for the species. This report is an example of the developing and highly collaborative process of Early Detection and Rapid Response (EDRR) to invasive species, involving many individuals, both professional and private, contributing key elements in a short period of time.

The first spontaneous plants of *Arum italicum* Mill. at NYBG were noted in the Thain Family Forest in 2004, but were not reported in the NYBG flora of 2016 (Atha et al. 2016) because their status as cultivated or spontaneous was not clear and they did not appear to be spreading. With additional sighting of plants in Manhattan and the accumulated evidence for their invasiveness elsewhere, it became evident that the NYBG plants were indeed invasive, thriving in our region, and posed a significant threat.

The spontaneous NYBG population is located on the Ridge Trail along the western edge of the Thain Family Forest, approximately 100 meters east of the Rock Garden. The vegetation is a mature, deciduous forest with *Prunus serotina, Quercus alba, Carya glabra,* and *Carya tomentosa* dominant. Understory vegetation consists of *Eurybia divaricata, Lonicera japonica, Smilax rotundifolia, Viburnum prunifolium,* and *Aralia elata.* We found two discrete patches, one about 50 cm diameter consisting of dozens of plants. A second patch, about 1.5 meters away consists of just two young stems. According to NYBG gardeners, three small patches of *Arum italicum* have been observed between the Rock Garden and the Thain Family Forest.

The Inwood Hill Park site is located in the Inwood section of Manhattan, about 100 meters north of Dyckman Street on a south-facing slope bisected by two paved paths/roads. We surveyed an area of about 2,500 square meters, roughly centered about where the Inwood Hill Park collection was made. In this area we began counting patches and stopped at over one dozen when it became apparent that there were dozens and dozens more patches and individuals scattered throughout the survey area, almost too numerous to count. Virtually any square meter, randomly placed could harbor a solitary or juvenile colony of *Arum italicum.* The vegetation consists of *Prunus serotina, Celtis occidentalis, Rhus typhina, Ailanthus altissima, Ulmus americana, Lonicera* shrubs*, Rosa multiflora, Vitis sp., Carya cordiformis, Tilia americana* (possibly planted)*, Alliaria petiolata, Galium aparine, Allium vineale, Lonicera japonica* and *Hedera helix.* For many years, the understory of the site was overgrown with a dense layer of *Lonicera* sp. and *Rhodotypos scandens.* In 2007, the shrub layer was cleared of invasives and *Quercus bicolor* and other trees were planted in the area. Clearing the shrub layer caused an explosion of invasive vines, particularly *Lonicera japonica* and *Hedera helix.* The *Arum italicum* plants were not noted by Park gardeners until this year, perhaps only after additional invasives, especially *Hedera helix* and *Lonicera japonica,* were removed and the ground layer exposed.

The Fort Tryon population consists of at least four separate infestations scattered over an area of roughly 20,000 square meters. There are several patches of *Arum italicum* in the Heather Garden, which consists of *Erica* species and numerous perennial herbaceous and woody ornamentals. There are several patches northwest of the New Leaf Cafe in mixed beds of native and exotic trees and shrubs. In the mixed beds the plants are often growing with *Hedera helix.* We found one plant growing in the dense shade of *Taxus baccata* shrub where the ground was densely covered by fallen *Taxus* needles.

Adjacent to Carl Schurz Park and Gracie Mansion, on the Upper East Side of Manhattan, the species has colonized an area of waste ground which is approximately 7 meters vertically below the promenade. This narrow strip of land, about 30 meters in length, is situated between the FDR tunnel and the East River. In February 2017 there were four separate colonies of plants; one was a large cluster, over 1 meter across. In summer this area of waste ground is completely overgrown with spontaneous vegetation, much of it tall and bushy, including *Phytolacca americana* and *Rumex crispus.* Numerous smaller plant species are present, including *Hedera helix* and *Taraxacum officinale.* Young trees of *Ailanthus altissima* were cut down from this patch of ground a number of years ago. A tall ladder and more than one worker would be required in order to access this area. A member of the Carl Schurz Conservancy commented that this strip of land was originally owned by the Department of Transportation, but was subsequently deeded to the NYC Parks and Recreation Department. In March 2017, a small cluster which may be a volunteer was photographed less than 100 m away from the piece of waste ground, in a gardened area next to the footpath that runs around the north side of Gracie Mansion.

In 2012, the species was reported on iNaturalist as growing near the northwestern corner of Ward's Island in the East River. This was planted as an ornamental in a challenging location where nothing else would grow; the gardeners are aware that the plant can spread aggressively. Currently there are no records of occurrences in the natural areas of Ward's Island and Randall's Island.

Voucher specimens and iNaturalist observations. New York. <u>Bronx Co.</u>: New York City, New York Botanical Garden, W of the Bronx River and N of Waring Avenue, Thain Family Forest, Ridge Trail, ca 100 m E of the Rock Garden, 40.864567°, -73.877209° (WGS84, ±25m), ca 36 m elev, 24 Feb 2017, *Atha 15915* (NY); Conservatories, 13 Apr 1906, *Taylor s.n.* (NY). <u>New York Co.</u>: New York City, Inwood Hill Park, N of Dyckman Street and W of Payson Avenue, N of the Payson Playground, 40.867920°, -73.928427° (WGS84, ±25m), ca 16 m elev, 28 Feb 2017, *Atha & Thornbrough 15516* (NY); Fort Tryon Park, between the Cloisters and Margaret Corbin Circle, E of the Henry Hudson Parkway, W of Margaret Corbin Drive, 40.861159°, -73.933071° (WGS84, ±25m), ca 67 m elev, 10 Mar 2017, *Atha & Kelly 15917* (NY); Carl Schurz Park and Gracie Mansion, E of the Promenade and adjacent to the East River, 40.775968°, -73.942207° (WGS84, ±15m), 20 Feb 2017, *Hewitt* (iNaturalist observation 5144676); 40.775962°, -73.942213° (WGS84, ±16m), 2 Mar 2017, *Hewitt* (iNaturalist observation 5211672); 40.775987°, -73.942184° (WGS84, ±5m), 8 Mar 2017, *Hewitt & Seltzer* (iNaturalist observation 5253692); W of the Promenade, 40.77656°, -73.942968° (WGS84, ±16m), 8 Mar 2017, *Hewitt & Seltzer* (iNaturalist observation 5254116); Wards Island, Harlem River Pathway, 40.790757°, -73.930551° (WGS84, ±52m), 7 Jun 2012, *jgall* (iNaturalist observation 2909338).

Description

Italian Lords and Ladies (*Arum italicum* Mill.) is a perennial herb native to parts of Europe, North Africa, and western Asia (Prime 1981; Boyce 1993; Verloove 2017). Four infraspecific taxa may be distinguished on the basis of life cycle, morphology, and geographic distribution (Boyce 1993). Three of the subspecies are narrowly restricted and only *A. italiucm* subsp. *italicum* has escaped cultivation in North America (Yatskievych 1999). It is characterized as having leaves that are winter-emergent, monomorphic, variegated or bicolorous with acute, hastate and divergent lobes and a spathe that is greenish-white to pale yellow (Boyce 1993). Cultivars with strongly variegated leaves including 'Chameleon', 'Cyclops', 'Gold Dust', 'Marmoratum', 'Tiny' and 'White Winter' are derived from *A.italicum* subsp. *italicum* (Boyce 1993). Flowering stage is reached in 4–7 years, generally after the plants accumulate a minimum biomass (Boyce 1993; Mendez & Obeso 1993; Meeuse 1989) and like many other Araceae, the inflorescences of *A.italicum* are capable of endogenous heat production and can generate as much as a 15° C temperature differential between the inflorescence and its surroundings. Metabolism of isobutyl amine produces odors similar to urine and dung, which is volatilized by the heat and attracts mainly olfactory, dung-breeding midges or flies (Meeuse 1989; Albre et al. 2003). In three sites in France, flies were the most abundant visitors, representing nearly 90% of the insects attracted to inflorescences of *A. italicum*. Psychodidae flies and some Sciaridae, Chironomidae, and Sphaeroceridae were the main Diptera groups trapped (Albre et al. 2003). Exclusion and artificial pollen transfer experiments show that cross-pollination is necessary for *A. italicum* to set seed (Albre et al. 2003). Birds are apparently unharmed by the berries and readily feed on them, especially ground-feeding birds and other than humans, are thought to be the primary seed dispersal agents (Boyce 1993; Prime 1981; Meeuse 1989; Verloove 2017). In Europe, birds reported to feed on *Arum* fruit include mistle thrush, song thrush, European blackbird, starlings, pheasant, common wood pigeons, finches, sparrows, and yellowhammers (Prime 1981; Meeuse 1989). In Seattle, quail and American robins are reported to eat the fruit and disperse the seed (Meeuse 1989). Young plants are pulled deeper by contractile roots by up to 5 cm per week (Meeuse 1989).

New York City plants are herbs forming circular patches 1 m or more in diameter, the plants densely crowded (Figure 2), sometimes consisting of dozens of individuals with the largest plants generally toward the center; stems erect from deeply buried rhizomes/tubers (Figures 3–5);

rhizomes/tubers dark brown outside and white inside (Figures 5–6); plants dividing by production of ovoid bud-tubers ca 1 cm diam (Figures 5 and 8); rhizome/tubers forming roots and shoots from the same point, so that the shoot must grow plagiotropically before becoming erect (Figure 4); older stems white at the base where buried, then becoming reddish near ground level (Figures 3–4); petioles green, strictly erect and crowded; new leaves forming from center of plant; older leaves large and fleshy, the veins and adjacent tissue white, the posterior lobes obtuse to rounded; inflorescences forming in late winter (Figure 7). In New York City today, the leaves emerge in late summer or early fall and stay green and lush-looking through the winter, despite occasional periods of cold and snow (Figure 9). During the summer the foliage dies back and only the inflorescences with their bright red and orange fruits remain, possibly hidden among other vegetation that has leafed out for the season.

In England, the species is most often associated with *Hedera helix*, which is thought to provide winter protection (Prime 1981). In Europe, the species prefers light shade, some shelter and slightly basic soil (Meeuse 1989) and in Belgium, the plants are said to prefer disturbed soils high in nitrogen (Verloove 2017).

Toxic compounds attributed to *Arum italicum* include (1) arin, a saponin which, as a class of compounds is hemolytic and very common in diverse lineages of plants, (2) a coniine-like alkaloid and nerve toxin similar to the toxin in *Conium maculatum*, (3) calcium oxalate, an irritant and calcium uptake blocker also very common in plants, and (4) cyanogenic glycosides, which can be transformed into the highly lethal hydrocyanic acid (HCN) (Prime 1980; Meeuse 1989). Mammals, including guinea pigs, rats, mice, dogs, badgers, and pigs, will starve to death rather than eat *A. italicum* (Prime 1981). Calcium oxalate is destroyed by heat and like other members of the family Araceae, especially *Colocasia esculenta* (taro), the tubers of *A. italicum* have been boiled and eaten in time of famine (Meeuse 1989).

Cultivation

The species has been cultivated in outdoor gardens throughout the USA at least since the mid-Twentieth century (Bailey 1942). Escaped populations in North America are reported with increasing frequency and spontaneous populations are now documented from Washington, Oregon, California, Illinois, Missouri, Alabama, Tennessee, Maryland, Virginia, Washington, D.C. (EDDMapS 2017, Figure 1), and now New York. Municipal, state, and federal efforts are underway to address the threat posed by this species (Briefel & Frey 2012; King Co., Washington 2016; City of Portland, Oregon 2017; Maryland Invasive Species Council 2017). *Arum italicum* is listed as a Class C noxious weed by the Washington State Noxious Weed Control Board (WSNWCB 2017). A 2-acre infestation on Lopez Island, San Juan Co., Washington "worsened after it was repeatedly mowed, dug, torched (in winter), and then covered with a heavy tarp" (WSNWCB 2017). In New Zealand, the species is regulated as a surveillance species to minimize further spread by preventing the sale, propagation, distribution, and exhibition of the species (Biosecurity New Zealand 2012).

Italian Lords and Ladies is valued by gardeners for its lush, winter foliage, attractive fruit and because it adds novelty to the Garden, in the sense that is relatively uncommon and nothing else looks quite like it. It is shade-tolerant, is extremely hardy and tolerates diverse edaphic conditions including a wide range of soil moisture, texture, etc. Gardeners in Westchester County, New York, report that it is not eaten by deer. These same traits also make it a very problematic invasive. The following quote from a gardener in Kentucky echos many contemporary gardeners' experiences and highlights the negative aspects of cultivation:

> "About 45 years ago, my parents planted a small clump of *Arum italicum* in a large wooded area of their central Kentucky yard. Over the years they also planted 30–40 species of native wildflowers that now blanket this grove every spring. For about 30 years, the *Arum* charmed everyone. Now? Not at all. In fact, *A. italicum* has become such a menace that in another 20

years none of those native wildflowers will be left. It will be a pure stand of *Arum*. I've tried digging it out but it's deeply rooted and it's impossible to capture the 100's of small bulbs. Weed-eating hasn't worked. Spraying with Glycophosphate [sic] hasn't worked. Our State forester researched the problem and gave me several articles but concluded there was not a known method of killing it. Another commenter mentioned Speedzone: I'll give that a try. I regard this plant as a sinister threat. It now pops up in far distant corners of this beautiful 10-acre yard. If you value native flora, I suggest not EVER planting *Arum italicum*" (Dave's Garden 2017).

In 1901 the NYBG obtained seed of *Arum italicum* from the Lyon Botanical Garden in France, grew them in a greenhouse, and in 1906 the plants were vouchered by Norman Taylor (*Taylor s.n.*). There is a record of another NYBG accession from 1931, but there is no information on location or current status. No specimens of *A. italicum* were noted or collected from cultivated or wild populations at NYBG between 1931 and 1989. Our experience has been that the species was not hardy outdoors in Cold Spring, New York (about 50 miles north of New York City), and there were no attempts to grow the plants outdoors at NYBG until very recently. However, beginning in 1989, the NYBG began accessioning plants for outdoor gardens (see Table 1).

Arum italicum subsp. *italicum*		
Accession	Year	Location at NYBG
2060/2004*A	2004	Perennial Garden - Shade Room (General)
1541/2005*A	2005	Home Gardening Center - Rodney White Country Garden
1519/2009*A	2009	Rock Garden - Meadow
2349/2010*A	2010	Azalea Garden - North 2
2403/2010*A	2010	Rock Garden - Heath
2403/2010*B	2010	Rock Garden - Heath
Arum italicum subsp. *italicum* 'Marmoratum'		
445/89*A	1989	Rock Garden - Woodland
1781/2012*A	2012	Rock Garden - Woodland
Arum italicum subsp. *italicum* 'White Winter'		
769/2009*A	2009	Perennial Garden - Shade Room (General)

Table 1. *Arum italicum* subspecies *italicum* and cultivars accessioned at NYBG since 1989.

Early detection and rapid response

The Early Detection and Rapid Response (EDRR) network of the Lower Hudson Partnership for Regional Invasive Species Management (LH PRISM) was mobilized to validate and document the occurrence of spontaneous populations of *Arum italicum* in two of New York City's important natural areas: the woodlands of Inwood Hill Park (New York county) and the Thain Family Forest of the New York Botanical Garden (NYBG) (Bronx county). Communication within the PRISM network and gardening community led to the identification of additional populations in Fort Tryon Park (spontaneous) and Wards Island (cultivated). Research on iNaturalist led to the addition of the population in Carl Schurz Park.

According to New York state's framework for Rapid Response for Invasive Species (NYS DEC 2016), the EDRR process should begin when a new infestation is reported to an agency or organization whose mission includes responding to invasions. Reports of probable spontaneous *Arum italicum* were recently brought to the attention of Steve Young, the state botanist with New York Natural Heritage, Program who shared the information on February 22, 2017, with the coordinator of the LH PRISM and NYBG botanists. Specific locations were indicated by New York City Parks botanists including Our first

step was to verify the report with onsite visits and voucher specimens. Once authenticated, the LH PRISM coordinator informed local resource managers via an alert sent out on the public listserve for the Lower Hudson PRISM on February 24. As suggested in the EDRR framework, we then performed rapid assessment of the extent of the infestation in New York City. Further assessment of the extent of the populations has begun and additional surveys of nearby properties are underway to delineate the full extent of the infestations. Following this assessment possible responses will be evaluated so that management plans can be drafted. The New York occurrences have also been entered into the New York iMapInvasives database.

Risks, control, eradication and garden alternatives

On 24 February 2017, the first author dug the NYBG specimens with a small trowel and by hand without gloves. After 48 hours, both hands began itching intensely as though exposed to Poison Ivy. By day four (28 Feb.) the itching had increased considerably (Figure 10). On 28 February, the split stem and rhizome/tuber in Figure 6 was experimentally applied to Atha's unaffected inner forearm (Figure 11). By 8:00 pm on 2 March, the area showed no sign of irritation. How to account for this differential reaction in the same person exposed to the same plant but on a different part of the body and from a different part of the plant is unknown. Perhaps the stems and rhizome/tubers do not possesses the same toxin or concentration of toxin as that exposed by digging the plants and handling the roots. Perhaps the underground parts of the plant were growing with *Toxicodendron radicans* roots. Further research is warranted.

The plant is extremely difficult to eradicate. It is not possible to pull it up because the stems break off above the tubers. Herbicides can kill the foliage, but the plants grow back from the tubers. When trying to dig up the plants, it is usually impossible to retrieve all the tubers, and so digging often simply results in spreading the plant. Planting in pots is not a good option either because the fruit would still be available to birds who could disperse seeds elsewhere.

Winter is the best time to search for and identify the plants as they are among the only herbaceous vegetation that is persistently green at this time. Other vegetation has generally lost its leaves, making it easier to spot among among other plantings. As in England, the most common associate in New York appears to be *Hedera helix*, which was observed at all New York sites. The *Hedera* could be providing winter insulation as well as camouflage. Like *Arum italicum*, *H. helix* is evergreen and persistent through the winter, forms dense colonies on the ground and has ovate, dark green, variegated leaves (Figure 12). *Arum italicum* could go undetected for quite some time, blending in with the *H. helix*.

There are native alternatives to *Arum italicum* suitable for cultivation in southeastern New York. *Asarum canadense*, *Cardamine diphylla*, and *Mertensia virginica* are low-growing ground-covers that are hardy, shade-tolerant and thrive in the urban environment in and around New York City. In wetter spots, *Arisaema triphyllum* could be used.

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Figure 1. Distribution of *Arum italicum* (EDDMapS, 2017).

Figure 2. *Arum italicum* at Inwood Hill Park showing clusters, each consisting of dozens of plants. Note variation in leaf variegation. Photographed on 28 February 2017.

Figure 3. *Arum italicum* whole plant showing above and below ground parts. *Atha & Thornbrough 15916.*

Figure 4. *Arum italicum* showing whole plant. Note plagiotropic growth of stem from tuber. *Atha & Thornbrough 15916.*

Figure 5. Fresh *Arum italicum* showing tubers and contractile roots (note rings on thicker roots).   *Atha & Thornbrough, 15916.*

Fig
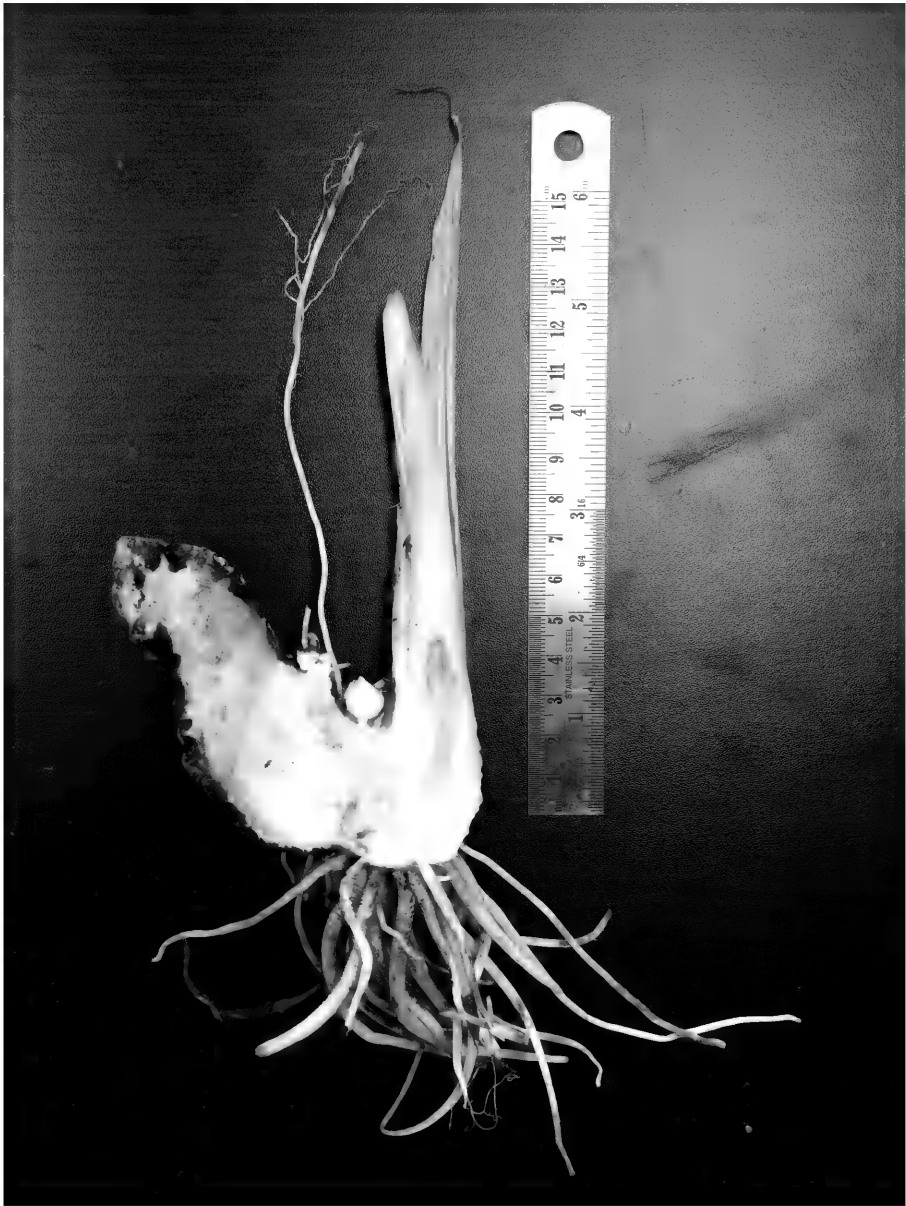
Figure 6. Fresh *Arum italicum* plant showing cross-section of rhizome/tuber, bud-tuber and stem. Note embryonic shoot in center (yellow-green), *Atha & Thornbrough 15916*.

Figure 7. Dried rhizome/tuber and stem in cross section showing embryonic inflorescence. *Atha & Thornbrough 15916.*

Figure 8. Dried rhizome/tuber and bud-tuber in cross-section, showing tuber with protective scales. *Atha & Thornbrough 15916.*

Figure 9. *Arum italicum* at Inwood Hill Park. Photographed on 10 March 2017.

Figure 10. Affected area five days after digging whole plant especially soil and roots from NYBG population *Atha 15914.*
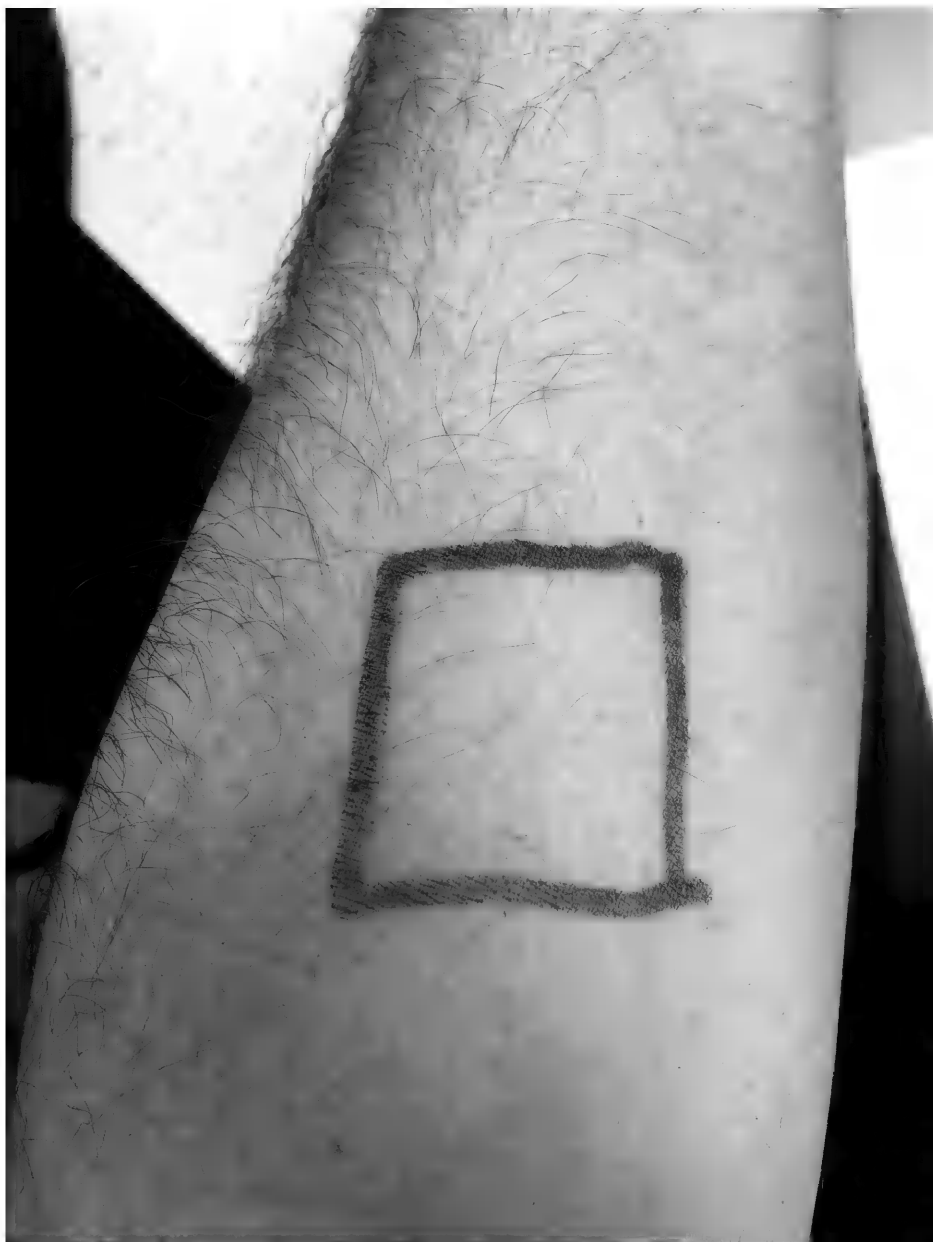
Figure 11. Exposed area apparently unaffected 48 hours after application of sap from cut rhizome/tuber and stem, from Figure 6.

Figure 12. *Arum italicum* growing together with *Hedera helix* at Fort Tryon Park, *Atha & Kelly 15917.*

SOLIDAGO ALTISSIMA VAR. PLURICEPHLA (ASTERACEAE: ASTEREAE) IN INDIA

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ABSTRACT
Herbarium collections of *Solidago* in Kew Herbarium from southern India are reported here to be *Solidago altissima* var. *pluricephala* M.C. Johnston, which is previously unreported for the country. An additional collection in JCB from Bangalore also is var. *pluricephala*. All specimens have densely hispid-strigose stems (sparsely to densely so proximally and densely so distally and in the inflorescence), lanceolate trinervate upper stem leaves with mostly entire or minutely serrate margins and moderately to densely strigose abaxial surfaces on the main and prominent lateral veins. Specimens of var. *pluricephala* have secund conical inflorescences that are much longer than wide, while those of var. *altissima* tend to be nearly as wide as long.

Solidago altissima L. is native to North American and is a member of *Solidago* subsect. *Triplinerviae* (Torr. & A. Gray) Nesom (Semple & Cook 2006). The species includes plants with densely hispid-strigose stems (sparsely to densely so proximally and densely so distally and in the inflorescence), lanceolate upper stem leaves with mostly entire margins (lower and mid stem leaves are usually serrate), and moderately to densely strigose abaxial surfaces on the main and prominent lateral veins. Three varieties are recognized and differ in distribution, upper leaf shape, size and number of upper stem leaf serrations, and inflorescence shape (Semple et al. 2015). The typical race ssp./var. *altissima* is common to abundant in the northern half of the eastern deciduous forest region of North America. Var. *pluricephala* M.C. Johnston is native to the southeastern USA from Maryland to Florida west to Oklahoma and south Texas. Subspecies/var. *gilvocanescens* (Rydb.) Semple is native to the prairies on the Great Plains from Alberta to Manitoba south to northern Texas; it also occurs in scattered prairie habitats further east. The typical race has been known to be invasive in Eurasia and Oceania for many years though often reported under *S. canadensis* L. or *S. canadensis* var. *scabra* (Muhl. ex Willd.) Torr. & Gray (China, Japan) or *S. altissima* (Chen & Semple 2011). Sakata et al. (2015) described how a few introductions could result in large scale invasion of *S. altissima* in Japan. Cheek and Semple (2016) documented the occurrence of var. pluricephala in South Africa. Verloove et al. (2017) recently documented the occurrence of var. *altissima* in Belgium.

Only hexaploids of *Solidago altissima* have been reported from South Asia (Sarkar et al. 1980; Bala and Gupta 2013, as *S. canadensis*), Japan (Huziwara, Y. 1962; Sakata et al. 2013a, b), and Taiwan (Peng & Hsu 1978). In North America, diploids and tetraploids occur in *S. altissima* var. *gilvocanescens* with a few tetraploids and predominantly hexaploids being reported for var. *altissima* and var. *pluricephala* (Semple et al. 2015).

During a visit to Kew Herbarium (K) in late 2014, a number of Eurasian and Oceanian collections of what appeared to be either *Solidago chilensis* or *S. altissima* were examined among the general collections of *Solidago*. These were borrowed from K for more detailed examination and scoring for comparison with specimens of the four species of *Solidago* known to be adventive in

countries outside North and South America (*S. altissima*, *S. canadensis*, *S. chilensis*, *S. gigantea*) and some of which were included in multivariate analyses (Semple et al. 2015; Lopez Laphitz & Semple 2015). Some *S. altissima* var. *pluricephala* plants from India have previously been misidentified as *S. canadensis* or *S. microglossa* DC.

Specimens of *Solidago altissima* var. *pluricephala* examined.   **INDIA.** Karnataka Prad. Bangalore, *Sankara Rao s.n.* (JCB HJCB028). Tamil Nadu Prad. Kodaikanal Dist., Palni (Pluney) Hills, Dindigul, Herb, 2 m; in garden planted along hedges, 2100 m, 7 Sep 1988, *Matthew s.n.* (K); Yercad Dist., Salem, Servarayans, loop road 2 km to Cuvery Peak, herb., escape from garden, 21 Mar 1979, *Venugopal & Jayaseelan s.n.* (K; Figs. 1 and 2).

The *Venugopal & Jayaseelan s.n.* (K) collection was included in a multivariate analysis of 291 specimens of *Solidago altissima*, *S. canadensis S. chilensis*, and *S. gigantea* following the methods described in Semple et al. (2015). The STEPWISE discriminant analysis selected 10 traits listed in decreasing order of F-to-remove values: outer phyllary length (25.65), length of disc floret corolla at anthesis (23.95), number of disc florets (11.05), upper stem leaf width (12.93), upper stem leaf length (11.38), number of mid stem leaf margin serrations (9.15), disc floret pappus length at anthesis (9.08), number of upper stem leaf margin serrations (8.98), disc corolla lobe length (8.80), disc floret achene body length at anthesis (8.49), and involucre height at anthesis (6.70). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of $p = 0.000$ that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 1. F-values based on Mahalanobis distances of the between group centroids indicated the largest separations were between *S. canadensis* and *S. chilensis* (81.691), and *S. altissima* and *S. chilensis* (71.206); the smallest separation was between *S. altissima* and *S. candensis* (29.843).

Table 1. Between groups F-matrix for the four a priori group analysis (df = 11   277).

Group	altissima	canadensis	chilensis
canadensis	29.843		
chilensis	71.206	81.691	
gigantea	41.147	31.344	57.754

Wilks' lambda = 0.0409 df = 119 3 287; Approx. F= 48.4692 df = 33 816 prob = 0.0000

In the Classificatory Discriminant Analysis of the *Solidago altissima*, *S. canadensis S. chilensis*, and *S. gigantea* species level a priori groups, a posteriori assignments of specimens ranged from 86-98% to their own group. The Classification matrix and Jackknife classification matrix are presented in Table 2. *Venugopal & Jayaseelan s.n.* (K; yellow stars in Fig. 3) was included in the *S. altissima* a priori group and was assigned a posteriori to the *S. altissima* group with 89% probability (11% to *S. chilensis*).

Two dimensional plots of CAN1 versus CAN3 and CAN1 versus CAN2 canonical scores for 69 specimens of *Solidago jejunifolia*, *S. pallida*, *S. rigidiuscula*, and *S. speciosa* are presented in Figure 12. Eigenvalues on the first three axes are 3.259, 1.099 and 0.774.

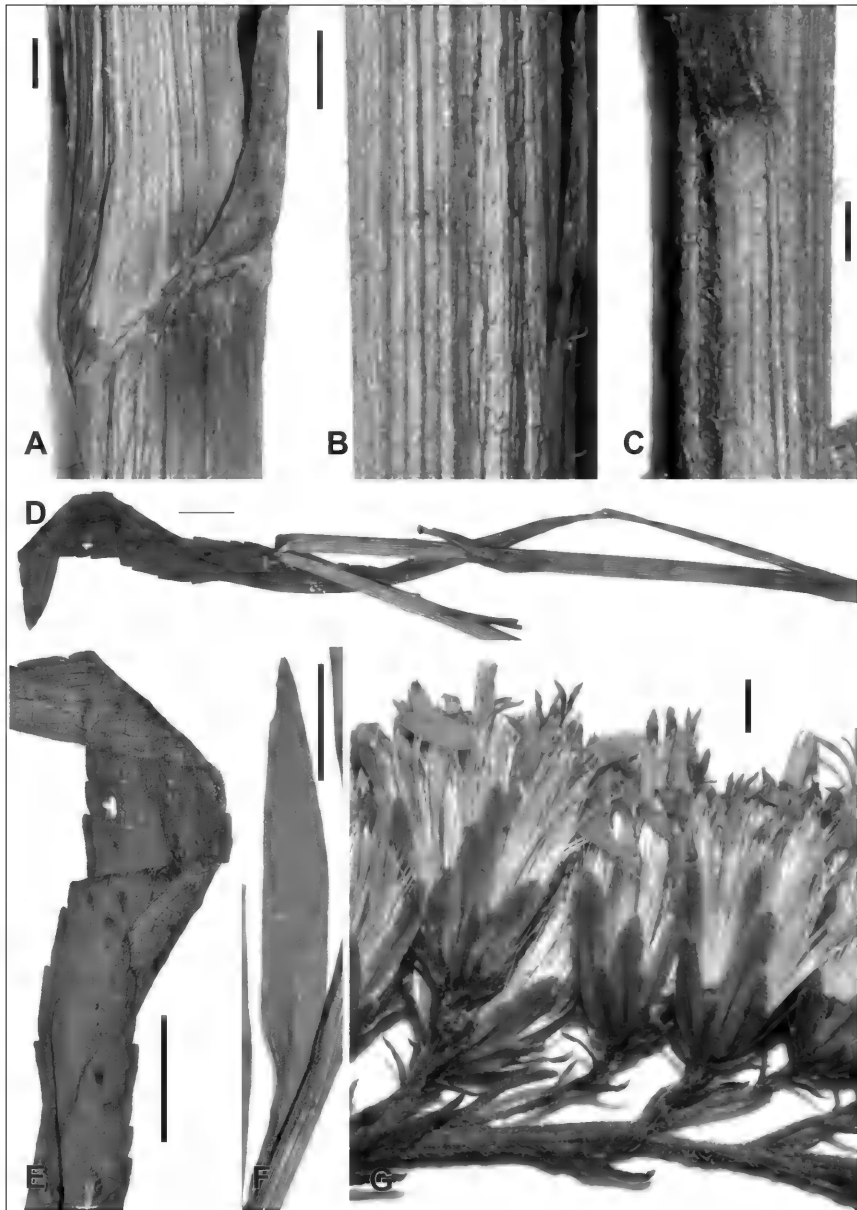Figure 1. *Solidago altissima* var. *pluricephala* from India: *Venugopal & Jayaseelan 22469* (K).

Figure 2. Details of *Solidago altissima* var. *pluricephala* from India: *Venugopal & Jayaseelan 22469* (K).
A. Lower stem. **B.** Mid stem. **C.** Upper stem. **D-E.** Lower stem leaf. **F.** Upper stem leaf. **G.** Heads on lower inflorescence branch. Scale bar = 1 mm in A-C, G; 1 cm in D-F.
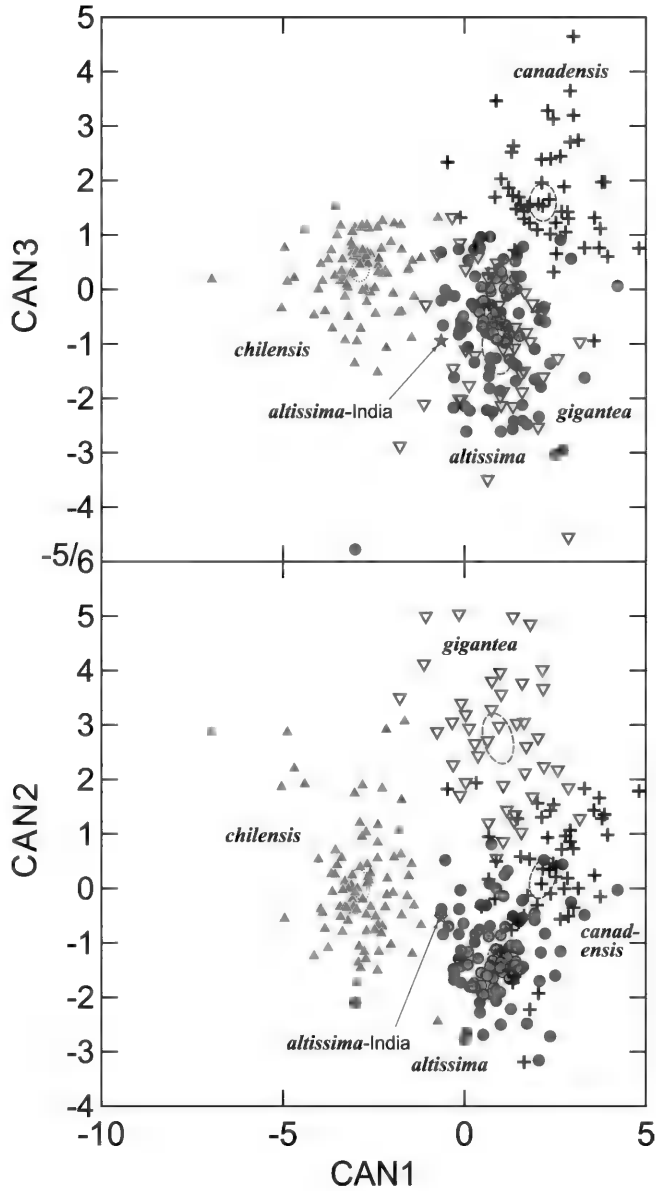
Figure 3. Plot of canonical scores (CAN1 vs CAN3 and CAN1 vs CAN2) for 291 specimens of adventive species of *Solidago*: *S. altissima* from India (yellow stars), *S. altissima* (red dots), *S. canadensis* (black +s), *S. chilensis* (blue triangles), and *S. gigantea* (green inverted open triangles).

Table 2. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of four a priori groups; a posteriori placements to groups in rows.

Group	altissima	canadensis	chilensis	gigantea	% correct
altissima	100	5	1	0	94
canadensis	4	49	0	4	86
chilensis	1	0	86	1	98
gigantea	0	1	0	39	98
Totals	105	55	87	44	94

Jackknifed classification matrix

Group	altissima	canadensis	chilensis	gigantea	% correct
altissima	96	6	2	2	91
canadensis	5	48	0	4	84
chilensis	1	1	85	1	97
gigantea	2	3	1	34	85
Totals	104	58	88	41	90

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MULTIVARIATE STUDIES OF *SOLIDAGO* SUBSECT. *SQUARROSAE*. II. THE *SOLIDAGO BICOLOR-S. HISPIDA* COMPLEX (ASTERACEAE: ASTEREAE)

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ABSTRACT

The *Solidago bicolor-S. hispida* complex in the broad sense includes six species in *Solidago* subsect. *Squarrosae*: *S. bicolor*, *S. erecta*, *S. hispida*, *S. porteri*, *S. roanensis*, and *S. sciaphila*. While generally rather similar, each species is distinguished by different sets of indument and leaf and floral traits. *Solidago bicolor* has whitish rays while the other five have yellow rays. *Solidago bicolor*, *S. erecta*, *S. hispida*, and *S. roanensis* are diploid while *S. sciaphila* is tetraploid and *S. porteri* is hexaploid. A series of multivariate morphometric analyses were performed to discover additional technical traits useful in separating species.

Solidago subsect. *Squarrosae* A. Gray (Asteraceae: Astereae) includes 14 species native primarily to eastern Canada and the midwestern and eastern portions of the USA (Semple et al. 2017). Semple and Cook (2006) recognized 9 species with infraspecific taxa in several species, while Semple (2017 frequently updated) recognized 14 species: *S. bicolor* L., *S. erecta* Pursh, *S. hispida* Muhl., *S. jejunifolia* Steele, *S. pallida* (Porter) Rydb., *S. porteri* Small, *S. puberula* Nutt., *S. pulverulenta* Nutt., *S. rigidiuscula* (Torr. & A. Gray) Porter, *S. roanensis* Porter, *S. sciaphila* Steele, *S. speciosa* Nutt., *S. squarrosa* Muhl., and *S. villosicarpa* LeBlond. Semple et al. (2017) informally divided the subsection into three species complexes based on a multivariate analysis of all 14 species and analyzed the *S. speciosa* complex in more detail. The *S. bicolor/S. hispida* complex includes the white rayed *S. bicolor* (Figs. 1-2) and the yellow rayed *S. hispida* (Figs. 3-4), *S. roanensis* (Figs. 5-6), *S. sciaphila* (Figs. 7-8), and *S. erecta* (Figs. 9-10), which was also included peripherally in the *S. speciosa* complex by Semple et al. (2017). *Solidago bicolor*, *S. hispida, S. roanensis*, and *S. erecta* are known only at the diploid level (Beaudry & Chabot 1959; Beaudry 1963, 1969; Kapoor 1970, 1977; Morton 1981; Semple et al. 1981, 1984, 1993; Love & Love 1982a; Semple & Chmielewski 1987; Semple and Cook 2004; unpublished data). *Solidago sciaphila* is the only tetraploid in the complex (unpublished data). The five species are overall morphologically similar but differ in stem hair density and distribution and differ in subtle ways in floral traits in addition to the obvious ray color difference. The very rare *Solidago porteri* is also most likely part of the *S. bicolor-S. hispida* complex but is readily recognized by it combination of large heads and stems that are glabrous proximally and sparsely to moderately hispid-strigose distally (see figures in Semple and Estes 2014). *Solidago porteri* is known from one location in south-central Tennessee, one location in northern Alabama, and several locations in central Georgia and is the only hexaploid in subsect. *Squarrosae* (Semple & Estes 2014).

The five species of the *Solidago bicolor/S. hispida* complex occur in overlapping ranges in eastern Northern America. *Solidago bicolor* occupies sandy, gravelly and loamy soils in open mixed woods, and wood and road margins and occurs from Nova Scotia and eastern Ontario south to Georgia and Alabama (Fig. 11). *Solidago hispida* occupies sandy or gravelly soils in open disturbed areas, crevices in rock outcrops, roadsides, prairies, woodland margins, open jack pine woods, and openings in mixed woods and is the most widely distributed species in the complex and (Fig. 12). *Solidago roanensis* (Fig. 13) occupies sandy or loamy, frequently moist, soils along roadsides, and on open rocky banks and mountain slopes, mixed deciduous woods and margins, oak-hemlock woods,

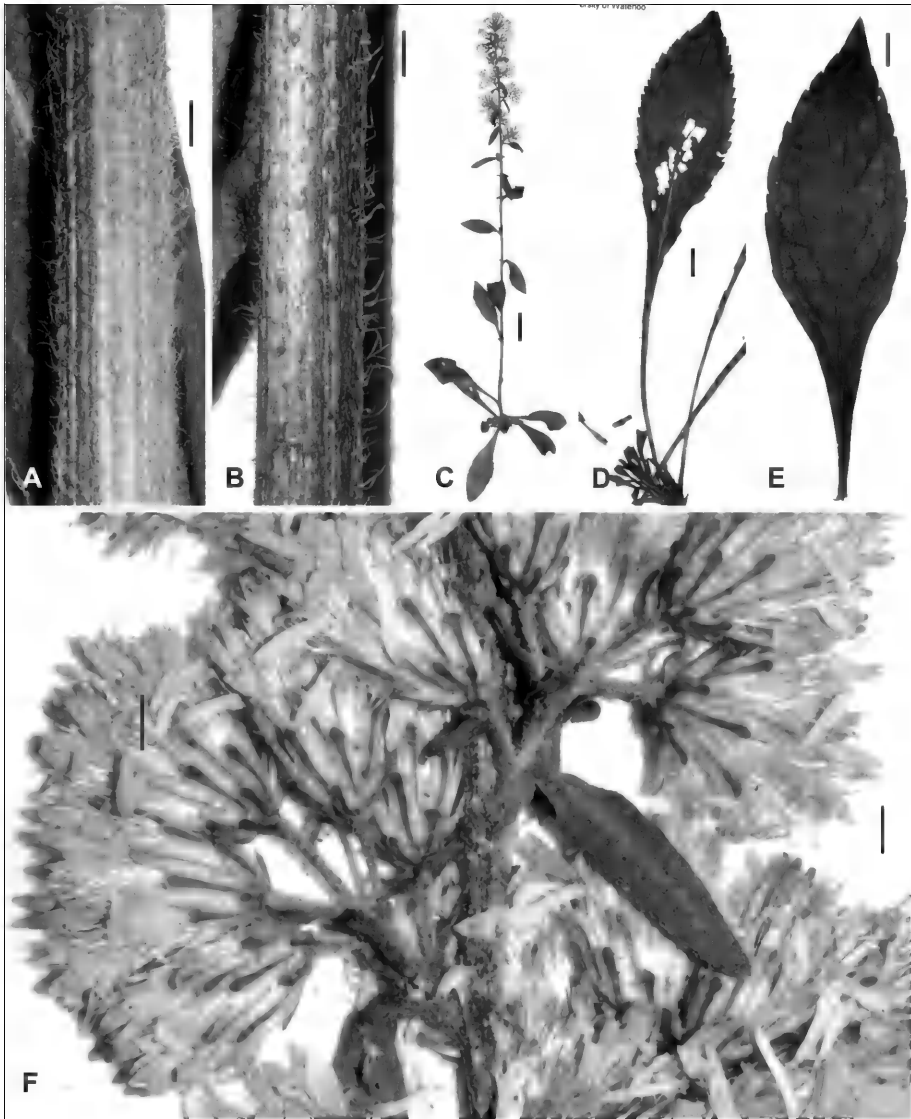Figure 1. Morphology of *Solidago bicolor*: *Semple & B. Semple 11510* (WAT), Queens Co., Nova Scotia.

Figure 2. Details of *Solidago bicolor*. **A-B.** Mid stem hair density variation. **A.** *Semple & Keir 4592* (WAT), Québec. B. *Semple 3705* (WAT), Connecticut. C. Dwarf shoot, *Shchepanek & Dugal 3788* (WAT), Prince Edward Island. **D.** Basal rosette leaf, *Semple 10732* (WAT), Virginia. **E.** Lower stem leaf, *Semple & Suripto 9839* (WAT), Georgia. **F.** Heads with white rays, *Semple 3705* (WAT). Scale bars = 1 mm in A-B, F; = 1 cm in C-E.

Figure 3. Morphology of *Solidago hispida*: *Semple & Brammall 2846* (WAT, Sudbury Dist., Ontario.

Figure 4. Details of *Solidago hispida*. **A-F.** Mid stem hair length and density variation. **A-E.** Var. *hispida*. **A.** *Hamel C68020* (MT), "var. *lanata*" with long dense woolly hairs), Québec. **B.** *Semple & Brammall 2846* (WAT), Ontario. **C.** *Arnett & Hastings 1081* (LSU), Louisiana. **D.** *Doucet Do-59-6-15* (MT), Québec. **E.** *Baldwin 11518* (WAT), short dense canescent hairs, Saskatchewan. **F.** Var. *huronensis*, glabrous stem; *Morton & Venn NA7682* (WAT), Ontario. **G.** Var. *tonsa*, very small plant; *Morton & Venn NA12186* (TRT), Newfoundland. **H.** Var. *hispid*a, heads with yellow rays, *Fernald 12165* (MT), Québec. Scale bars = 1 mm in A-F and H; = 1 cm in G.

Figure 5. Morphology of *Solidago roanensis*: *Biltmore Herbarium 4622* (NY), Buncombe Co., North Carolina.

Figure 6. Details of **Solidago roanensis**. **A-B.** Lower and mid stems, *Radford 6481* (NCU), North Carolina. C. Mid stem, *Cannon 213* (NY), North Carolina. **D.** Multiveined phyllaries, *Cannon 213* (NY). **E.** Basal rosette, *Cusick 26911* (NY), West Virginia. **F.** Heads with yellow rays, *Poindexter 05-1937* (WAT), North Carolina. Scale bars = 1 mm in A-D, F; = 1 cm in E.

Figure 7. Morphology of *Solidago sciaphila*: *Zager 921005-6* (MIN), Houston Co., Minnesota.
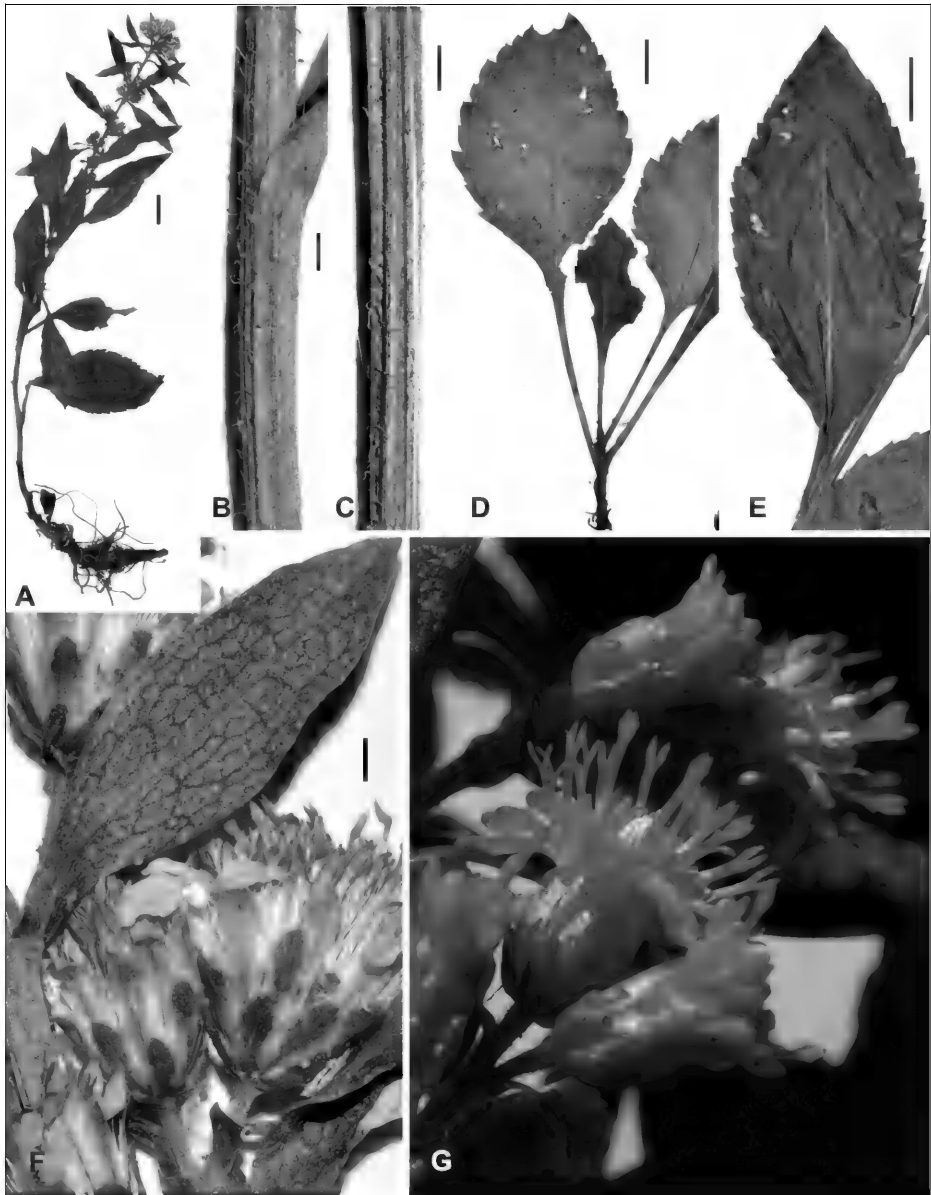
Figure 8. Details of the morphology of *Solidago sciaphila*. **A-D**. *Semple 11854* (WAT), Illinois. **A.** Small shoot. **B-C.** Lower and mid stem. **D**. Basal rosette leaves. **F-G**. *Semple 11851* (WAT),Wisconsin. **F.** Heads and bract, dried herbarium sheet. **G.** Heads, fresh in field. Scale bars = 1 mm in B-C, F; = 1 cm in A, D-E.

Figure 9. Morphology of *Solidago erecta*: *Semple 10771* (WAT) Sullivan Co., Tennessee.

Figure 10. Details of the morphology of *Solidago erecta*: *Semple 10771* (WAT), Sullivan Co., Tennessee. **A.** Lower stem. **B.** Mid stem. **C.** Stem in inflorescence, peduncles and head. **D.** Heads, rays yellow when fresh. Scale bars = 1 mm.
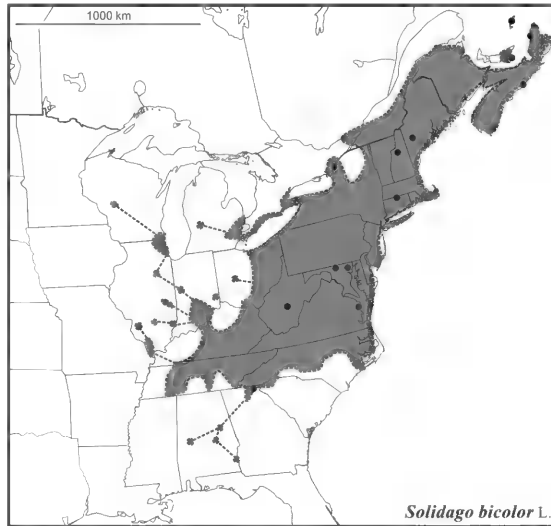
Figure 11. Range of distribution of *Solidago bicolor* and locations of specimens included in the analyses.
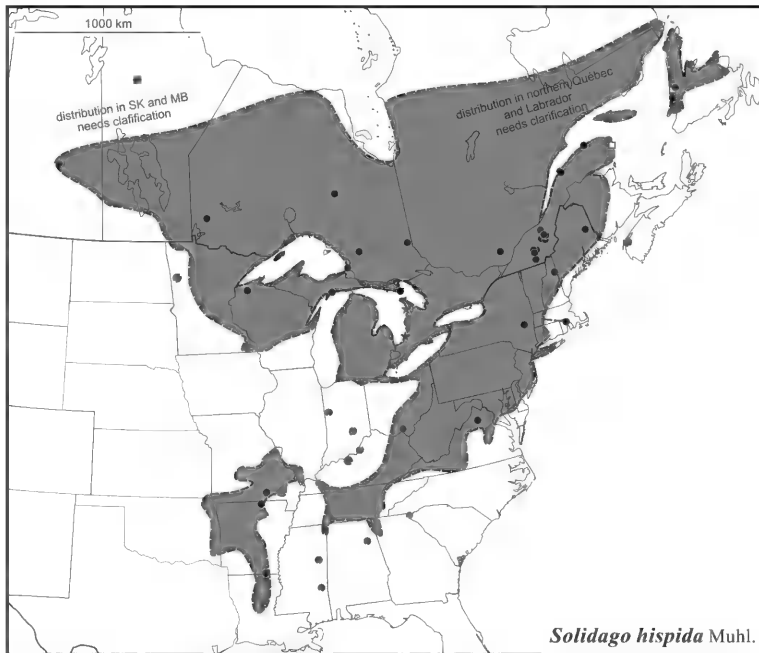

Figure 12. Range of distribution of *Solidago hispida* and locations of specimens included in the analyses: *var. arnoglossa* (red dots), var. *hispida* (black dots), var. *huronensis* (black stars), and *var. tonsa* (white squares).
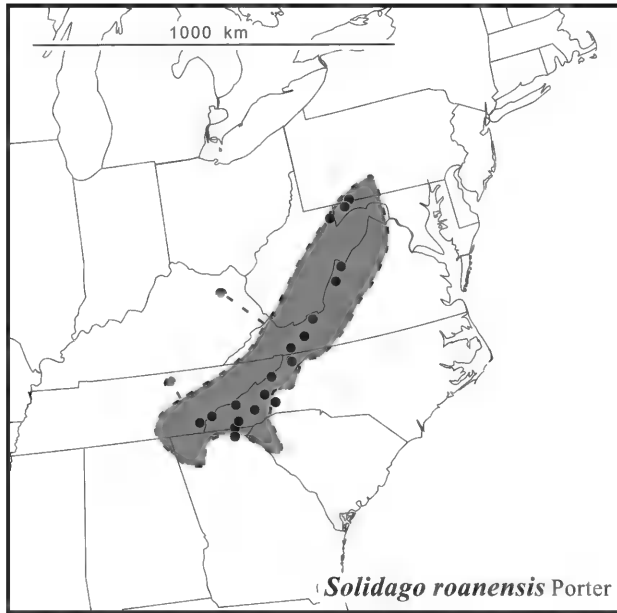
Figure 13. Range of distribution of *Solidago roanensis* and locations of specimens included in the analyses.
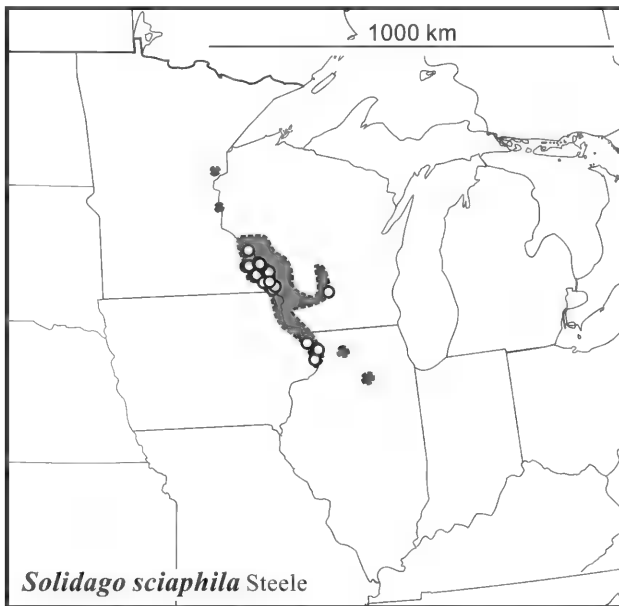

Figure 14. Range of distribution of *Solidago sciaphila* and locations of specimens included in the analyses.
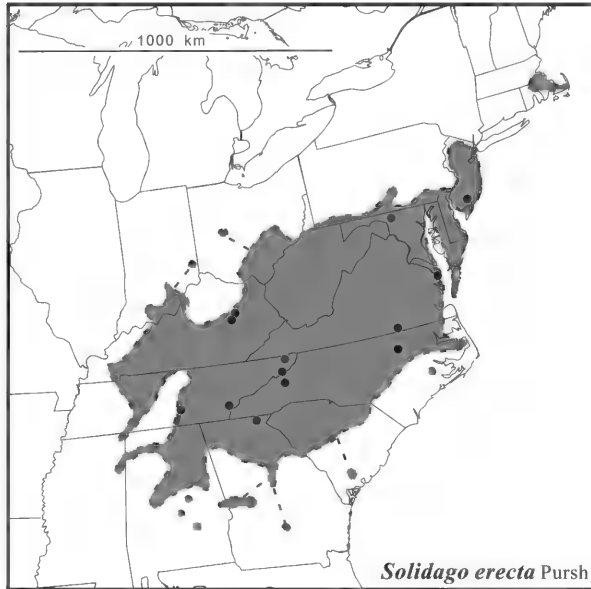
Figure 15. Range of distribution of *Solidago erecta* and locations of specimens included in the analyses.

and it occurs in the Appalachian Mountains from Pennsylvania to northern Georgia and Alabama. *Solidago sciaphila* occupies moist to dry rocky limestone and sandstone bluffs, dry dolomite cliff faces, in mixed pine and deciduous woods and margins, and is confined to much of the Driftless Area or Paleozoic Plateau of southwestern Wisconsin and adjacent states making it the only upper Midwestern species in the complex (Fig. 14). *Solidago erecta* occupies sandy clay and sandy loamy soils in open woods, along roadsides and road embankments, steep woody slopes, wet mixed hardwoods, cedar glades, and open pine woodlands on granite, and occurs at low to high elevations from Massachusetts to Georgia and northern Mississippi (Fig. 15) being generally more inland further south.

       Solidago hispida is the most morphologically variable species in the complex and historically has been divided into eight varieties by multiple authors primarily on differences in stem and leaf indument: var. *arnoglossa* Fern., var. *disjuncta* Fern., var. *hispida*, var. *huronensis* Semple, var. *lanata* (Hook.) Fern, var. *luteola* Farwell, var. *ovalis* Farwell, and var. *tonsa* Fern. *Solidago hispida* itself has been treated as a variety within *S. bicolor*: *S. bicolor* L. var. *concolor* Torrey & A. Gray, *S. bicolor* var. *hispida* (Muhl.) B.S.P. Var. *arnoglossa* and var. *tonsa* were described from small to mid-sized less-hairy plants from Newfoundland (Fig. 4G). Var. *huronensis* was described from glabrous/ glabrate stemmed plants (Fig. 4F) native to sand dunes along the eastern shore of Lake Huron in Ontario; Fernald (1950) had included these plants in his var. *tonsa*. These three varieties appear to represent ecotypes adapted to local conditions within limited portions of the range of the species. Var. *lanata* was described from the western limits of the range in Saskatchewan (*Drummond s.n.*, GH ex Herb. Benth.!) and has the most densely woolly indument on stems occurring in the species. Fernald (1950) recognized var. *lanata* as occurring from Newfoundland to Saskatchewan across Canada. Densely woolly specimens collected in Ontario and Québec (Fig 4A) were included in this study. Stem hair density grades down to sparsely hispid-woolly stems (Figs. 4B-D). Sometimes the stem hairs are very short and the stems are canescent (Fig. 4E). With no obvious discontinuities in

stem hair density and length, most of these various indument forms have been lumped into var. *hispida* (Semple & Cook 2006). Included in the large sample of *S. hispida* in this study were specimens representing var. *arnoglossa*, var. *hispida* (including var. *lanata*), var. *huronensis*, and var. *tonsa*. Semple and Cook (2006) concluded that "other varietal names are based on minor variations".

No multivariate study of *Solidago hispida* or the entire *S. bicolor/S. hispida* complex has been previously published. The purpose of the study presented here is to compare and contrast morphological differences among the six species included in the complex using statistical methods.

MATERIALS AND METHODS

In total, 261 specimens from BALT, BOON, GA, LSU, MO, the J.K. Morton personal herbarium now deposited in TRT, MIN, MT, NCU, NEBC, NY, TAWES, UNB, and WAT in MT (Thiers, continuously updated) were scored and included in the analyses: *Solidago bicolor* (17 specimens), *S. erecta* (19 specimens), *S. hispida* (76 specimens representing four putative varieties), *S. porteri* (11 specimens), *S. roanensis* (20 specimens), *S. sciaphila* (20 specimens), and *S. speciosa* (23 specimens included in Semple et al. 2017). These were selected from more than 1700 specimens of *S.* subsect. *Squarrosae* examined. For each specimen, 18 vegetative and 19 floral traits were scored when possible: 1-5 replicates per character depending upon availability of material and whether or not the trait was meristic (Table 1). Basal rosette leaves were often not present. Lower stem leaves were sometimes not present. Mean values were used in the analyses, while raw values were used to generate ranges of variation for each trait. All traits scored are listed in Table 1.

All analyses were performed using SYSTAT v.10 (SPSS 2000). Details on the methodology were presented in Semple et al. (2016) and are not repeated here. Eight analyses were performed. In the <u>first</u> analysis, *Solidago bicolor*, *S. erecta*, *S. hispida*, *S. porteri*, *S. roanensis*, and *S. sciaphila* were included in STEPWISE discriminant analysis. In the <u>second</u> analysis, *S. bicolor*, *S. erecta*, *S. hispida*, *S. roanensis*, and *S. sciaphila* were included in a STEPWISE discriminant analysis. In the <u>third</u> analysis, *S. bicolor*, *S. roanensis*, and *S. sciaphila* were included in a STEPWISE discriminant analysis. In the <u>fourth</u> analysis, *S. bicolor*, *S. hispida*, *S. roanensis* were included in a STEPWISE discriminant analysis. In the <u>fifth</u> analysis, *S. hispida*, *S. sciaphila*, and *S. speciosa* were included in a STEPWISE discriminant analysis. In the <u>sixth</u> analysis, just *S. bicolor* and *S. hispida* were included in a STEPWISE discriminant analysis. In the <u>seventh</u> and <u>eighth</u> analyses on *S. hispida*, var. *arnoglossa*, var. *hispida*, var. *huronensis* and var. *tonsa* were included in STEPWISE discriminant analyses with different sets of characteristics.

Table 1. Traits scored for the multivariate analyses of 261 specimens of *Solidago* subsect. *Squarrosae*.

Abbreviation	Description of trait scored
STEMHT	Stem height measured from the stem base to tip (cm)
BLFLN	Basal rosette leaf length including petiole (mm)
BLFPETLN	Basal rosette leaf petiole length (not scored if winged margins broad)
BLFWD	Basal rosette leaf width measured at the widest point (mm)
BLFWTOE	Basal rosette leaf measured from the widest point to the end (mm)
BLFSER	Basal rosette leaf-number of serrations on 1 side of margin
LLFLN	Lower leaf length measured from the leaf base to tip (mm)
LLFWD	Lower leaf width measured at the widest point (mm)
LLFWTOE	Lower leaf measured from the widest point to the end (mm)
LLFSER	Lower leaf dentation-number of serrations of lower leaf

MLFLN	Mid leaf length measured from the leaf base to tip (mm)
MLFWD	Mid leaf width measured at the widest point (mm)
MLFWTOE	Mid leaf measured from the widest point to the end (mm)
MLFSER	Mid leaf dentation-number of serrations of mid leaf
ULFLN	Upper leaf length measured form the leaf base to tip (mm)
ULFWD	Upper leaf width measured at the widest point (mm)
ULFWTOE	Upper leaf measured from the widest point to the end (mm)
ULFSER	Upper leaf dentation-number of serrations of upper leaf
CAPL	Length of inflorescence (cm)
CAPW	Width of inflorescence (cm)
INVOLHT	Involucre height (mm)
OPHYLN	Outer phyllary length (mm)
OPHYLW	Outer phyllary width (mm)
IPHYLN	Inner phyllary length (mm)
IPHYLW	Inner phyllary width (mm)
RAYNUM	Number of ray florets per head
RLAMLN	Ray strap length top of the corolla tube to the tip of the strap (mm)
RLAMPWD	Ray strap width measured at the widest point (mm)
RACHLN	Ray floret cypsela body length at anthesis (mm)
RPAPLN	Ray floret pappus length at anthesis (mm)
DCORLN	Disc floret corolla length from the base to tip of the corolla lobes (mm)
DLOBLN	Disc floret corolla lobe length lobe (mm)
DACHLN	Disc floret achene length at anthesis (mm)
DPAPLN	Disc floret pappus length at anthesis (mm)

RESULTS

The Pearson correlation matrix yielded r > |0.7| for most pairs of leaf traits reducing the number to be used to either mid leaf length, mid leaf width, or mid leaf serrations. Basal rosette leaves were often absent and were not included in the discriminant analyses: basal leaf length, petiole length, and length from widest point to tip were all highly correlated. Lower leaves were sometimes absent and lower leaf traits were excluded from discriminant analyses. Ray floret pappus body length at anthesis correlated highly with disc floret pappus length and only the latter trait was included in discriminant analysis of *Solidago bicolor*, *S. roanensis* and *S. sciaphila*, but these traits did not correlate as highly in the other combinations of taxa and were included in the analyses. Inflorescence length and width traits were highly variable in all species and were not included in the analyses.

Six species a priori groups analysis

In the STEPWISE discriminant analysis of 161 specimens of six species level a priori groups (*Solidago bicolor*, *S. erecta*, *S. hispida*, *S. porteri*, *S. roanensis*, and *S. sciaphila*), the following ten traits were selected as best separating the groups and are listed in order of decreasing F-to-remove values: number of ray florets (15.12), ray floret pappus length at anthesis (13.13), disc corolla lobe length (11.69), ray floret lamina length (7.50), number of disc florets (6.80), disc floret pappus length at anthesis (6.28), mid stem leaf width (6.10), inner phyllary length (5.90), outer phyllary length (5.81), and upper leaf margin serrations (3.99). Wilks's lambda, Pillai's trace, and Lawley-Hotelling

trace tests of the null hypothesis that all groups were samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 2. F-values based on Mahalanobis distances between group centroids indicated the largest separations were between *S. porteri* and *S. hispida* (33.750), *S. porteri* and *S. roanensis* (31.233), and *S. porteri* and *S. sciaphila* (30.292), and the least separations were between *S. roanensis* and *S. sciaphila* (3.282) and *S. bicolor* and *S. hispida* (3.738).

In the Classificatory Discriminant Analysis of the six species level a priori groups (*Solidago bicolor*, *S. erecta*, *S. hispida*, *S. porteri*, *S. roanensis*, and *S. sciaphila*), percents of correct a posterori assignment to the same a priori group ranged from 63-100%. The Classification matrix and Jackknife classification matrix are presented in Table 3. Results are presented in order of decreasing percents of correct placement. All 11 specimens of the *S. porteri* a priori group (100%) were assigned a posteriori into the *S. porteri* group; 10 specimens with 100% probability, and 1 specimen with 96% probability. Fifteen of the 18 specimens of the *S. erecta* a priori group (83%) were assigned a posteriori to the *S. erecta* group; 13 specimens with 94-100% probability, and 1 specimen with 89% probability, and 1 with 69% probability (25% to *S. hispida*). Three specimens of the *S. erecta* a priori group were assigned to other species: 1 specimen to *S. sciaphila* with 94% probability (*Semple & Suripto 9688* WAT from Mt. Mitchell, North Carolina); 1 specimen to *S. hispida* with 54% probability (18% to *S. sciaphila*, 15% to *S. roanensis*, and 12% to *S. bicolor*; *Semple & Ringius 7659* WAT from Washington Co., Maryland); and 1 specimen to *S. hispida* with 37% probability (36% to *S. sciaphila*, 21% to *S. erecta*, and 5% to *S. roanensis*; *Kral 37937* WAT from St. Clair Co., Alabama; in the *S. erecta-S. rigidiuscula-S. speciosa* analysis in Semple et al. 2017 this was placed into *S. erecta* with 50% probability and into *S. rigidiuscula* with 49% probability). Thirteen of 17 specimens of *S. bicolor* (76%) were assigned a posteriori to the *S. bicolor* group: 4 specimens with 90-98% probability, 3 specimens with 83-88% probability, 4 specimens with 70-78% probability, and 2 specimens with 49% probability (49% to *S. hispida*; *Oldham 22125* WAT from the Magdalene Is., Québec) and 46% probability (41% *S. hispida* and 6% each to *S. erecta* and *S. roanensis*; *Shchepanek 3788* WAT from Kings Co., Prince Edward Island). Four specimens of the *S. bicolor* a priori group were assigned a posteriori to three other species groups: 2 specimens to *S. hispida*, 1 specimen with 72% probability (22% to *S bicolor* and 4% to *S. sciaphila*; *Semple 10676* WAT from Greene Co., Pennsylvania) and 1 specimen with 45% probability (32% to *S. sciaphila* and 19% to *S. bicolor*; *Semple & Suripto 9839* WAT from Towns Co., Georgia); 1 specimen to *S. roanensis* with 62% probability (19% to *S. sciaphila* and 16% to *S. hispida*; *Semple 10656* WAT from Leeds Co., Ontario); and 1 specimen to *S. erecta* with 57% probability (27% to *S. bicolor* and 15% to *S. hispida*; *Semple 10732* WAT from Alleghany Co., Virginia). Fifteen of the 20 specimens of the *S. sciaphila* a priori group (75%) were assigned a posteriori to the *S. sciaphila* group: 3 specimens with 94-95% probability, 4 specimens with 85-89% probability, 1 specimen with 76% probability, 4 specimens with 66-68% probability, 2 specimens with 56% probability (28% to *S. hispida* and 14% to *S. roanensis*; *Dunevitz 911* MIN from Winona Co., Minnesota) and 55% probability (39% to *S. hispida*; *Dunevitz 1065* MIN from Wabash Co., Minnesota), and 1 specimen with 49% (*Zager 930907-5* MIN from Houston Co., Minnesota). Five specimens of the *S. sciaphila* a priori group were assigned a posteriori to other species groups: 4 specimens to *S. roanensis* with 85% probability (14% to *S. sciaphila*; *Smith 14946* MIN from Houston Co., Minnesota), 59% probability (38% to *S. sciaphila*; *Tenney 545* MIN from Winona Co., Minnesota), 50% probability (48% to *S. sciaphila*; *Dunevitz 637* MIN from Winona Co., Minnesota), and 1 specimen with 38% probability (36% to *S. sciaphila* and 25% to *S. hispida*; *Dunevitz 693* MIN from Winona Co., Minnesota); and 1 specimen to *S. erecta* with 75% probability (14% to *S. hispida* and 8% to *S. sciaphila*; *Dunevitz 978* MIN from Winona Co., Minnesota). Twelve of 19 specimens of the *S. roanensis* a priori group (63%) were assigned a posteriori to the *S. roanensis* group: 8 specimens with 92-99% probability, 1 specimen with 71% probability, 2 specimens with 67% and 63% probabilities, and 1 specimen with 54% probability (46%

to *S. sciaphila*; *Biltmore Herb. 4622b* NY from Rutherford Co., North Carolina). Seven specimens of the *S. roanensis* a priori group were assigned to two other species: 4 specimens to *S. sciaphila* with 88% probability (10% to *S. roanensis*; *Poindexter 05-1580* BOON from Ashe Co., North Carolina), 81% probability (10% to *S. roanensis* and 7% to *S. hispida*; *Williams s.n.* NY from Clay Co., North Carolina), 78% probability (22% to *S. roanensis*; *Cannon 213* NY from Avery Co., North Carolina), and 75% probability (*Biltmore Herb. 4622* NY from Buncombe Co., North Carolina); 3 specimens were assigned to *S. hispida* with 82% probability (6% each to *S. bicolor* and *S.* sciaphila and 5% to *S. roanensis*; *Radford 6481* NCU from Macon Co., North Carolina; phyllaries 1-veined), 65% probability (22% to *S. roanensis* and 13% to *S. bicolor*; *Boone s.n.4* TAWES from Garrett Co., Maryland), and 45% probability (36% to *S. roanensis* and 16% to *S. bicolor*; *Rydberg 8064* NY from Smyth Co., Virginia; phyllaries 1-veined); all 7 specimens had glabrous-glabrate lower stems, moderately to moderately dense hispid-strigose upper stems; and 5 of the 7 had multi-veined phyllaries. Forty-eight of 76 specimens of the *S. hispida* a priori group (63%) were assigned a posteriori to the *S. hispida* group: 4 specimens with 90-93% probability, 9 specimens with 81-87% probability, 16 specimens with 71-78% probability, 6 specimens with 60-68% probability, and 9 specimens with 50-59% probability. Twenty-eight specimens of the *S. hispida* a priori group were assigned to other species: 13 specimens were assigned to *S. bicolor* with 95-49% probability; 7 specimens were assigned to *S. sciaphila* with 95-49% probability; 5 specimens were assigned to *S. roanensis* with 81-41% probability, and 3 specimens were assigned to *S. erecta* with 88%, 67% and 61% probabilities.

Two dimensional plots of CAN1 versus CAN3 and CAN1 versus CAN2 canonical scores for 161 specimens of *Solidago bicolor*, *S. erecta*, *S. hispida*, *S. porteri*, S. *roanensis*, and *S. sciaphila* are presented in Fig. 16. Eigenvalues on the first three axes were 2.909, 0.920 and 0.56.

Table 2. Between groups F-matrix for the three a priori group analysis (df = 10   146).

Group	bicolor	erecta	hispida	porteri	roanensis
erecta	8.498				
hispida	3.738	13.173			
porteri	21.007	14.952	33.750		
roanensis	7.774	14.887	8.819	31.233	
sciaphila	10.762	13.195	8.637	30.292	3.282

Wilks' lambda = 0.0603 df = 10 5 155; Approx. F= 11.3889 df = 50 669 prob = 0.0000

Table 3. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of six a priori groups; a posteriori placements to groups in rows.

Group	bicolor	erecta	hispida	porteri	roanensis	sciaphila	% correct
bicolor	13	1	2	0	1	0	76
erecta	0	15	2	0	0	1	83
hispida	13	3	48	0	5	7	63
porteri	0	0	0	11	0	0	100
roanensis	0	0	3	0	12	4	63
sciaphila	0	1	0	0	4	15	75
Totals	26	20	55	11	22	27	71

Jackknifed classification matrix

Group	bicolor	erecta	hispida	porteri	roanensis	sciaphila	% correct
bicolor	9	1	6	0	1	0	53
erecta	0	15	1	0	0	2	83
hispida	15	3	46	0	5	7	61
porteri	0	1	0	10	0	0	91
roanensis	0	0	3	0	11	5	58
sciaphila	0	1	2	0	5	12	60
Totals	24	21	58	10	22	26	64
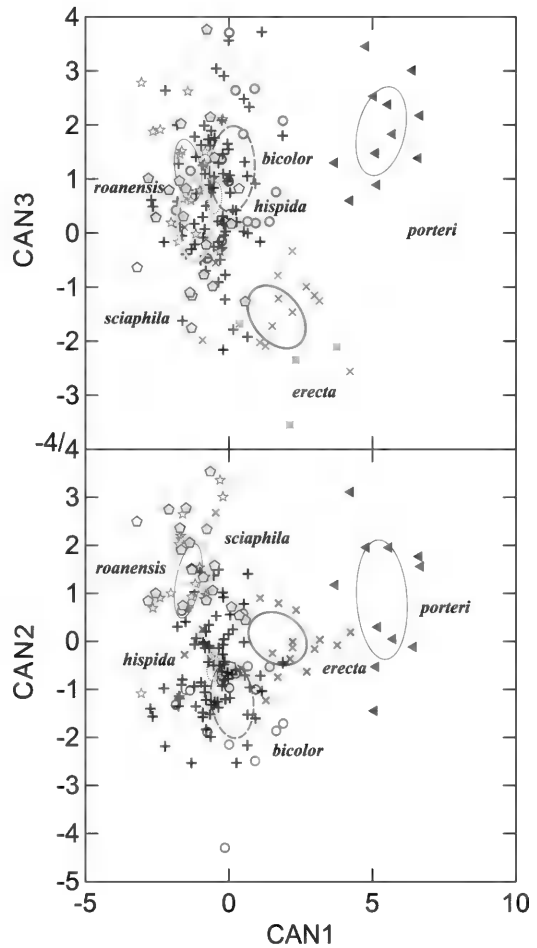
Figure 16. Plot of canonical scores (CAN1 vs CAN3 and CAN1 vs CAN2) for 161 specimens of *Solidago* subsect. *Squarrosae*: *S. bicolor* (red circles), *S. erecta* (green ×s, *S. hispida* (black +s), *S. porteri* (red triangles), *S. roanensis* (open blue stars), and *S. sciaphila* (pink pentagons).

Five species a priori groups analysis

In the STEPWISE discriminant analysis of 150 specimens of five species level a priori groups (*Solidago bicolor*, *S. erecta*, *S. hispida*, *S. roanensis*, and *S. sciaphila*), the following six traits were selected as best separating the groups and are listed in order of decreasing F-to-remove values: disc floret pappus length at anthesis (25.94), number of ray florets (16.50), ray floret lamina length (10.19), mid stem leaf width (6.38), outer phyllary length (6.08), and inner phyllary length (5.43). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 4. F-values based on Mahalanobis distances between group centroids indicated the largest separation was between *S. erecta* and *S. roanensis* (20.807), and the least separations were between *S. roanensis* and *S. sciaphila* (3.110) and *S. bicolor* and *S. hispida* (5.328).

Table 4. Between groups F-matrix for the five a priori groups analysis (df = 6   140).

Group	bicolor	erecta	hispida	roanensis
erecta	13.253			
hispida	5.328	18.603		
roanensis	12.702	20.807	12.968	
sciaphila	15.668	17.751	13.062	3.110

Wilks' lambda = 0.1992 df = 6 4 145; Approx. F= 11.9813 df = 24 489 prob = 0.0000

In the Classificatory Discriminant Analysis of 150 specimens of the five species level a priori groups (*Solidago bicolor*, *S. erecta*, *S. hispida*, *S. roanensis*, and *S. sciaphila*), percents of correct a posterori assignment to the same a priori group ranged from 55-83%. The Classification matrix and Jackknife classification matrix are presented in Table 5. Results are presented in order of decreasing percents of correct placement. Fifteen of 18 specimens of the *S. erecta* a priori group (83%) were assigned a posteriori into the *S. erecta* group; 12 specimens with 90-100% probability, 1 specimen with 84% probability, and 2 specimens with 67% and 61% probabilities. Three specimens of the *S. erecta* a priori group were assigned to other species: 1 specimen to *S. sciaphila* with 84% probability (14% to *S. roanensis*; Semple & Surpito 9688 WAT from Mt. Mitchell, North Carolina; lower and mid stems are glabrous); and 2 specimens to *S. hispida* with 43% probability (26% to *S. erecta* and 18% to *S. sciaphila*; Kral 37937 WAT from St. Clair Co., Alabama) and 41% probability (29% to *S. bicolor*, 24% to *S. roanensis*, and 6% to *S. sciaphila*; Semple & Ringius 7659 WAT from Washington Co., Maryland). Thirteen of the 17 specimens of the *S. bicolor* a priori group (76%) were assigned a posteriori to the *S. bicolor* group; 3 specimens with 92-93% probability, 6 specimens with 82-88% probability, 2 specimens with 76% and 61% probabilities, and 2 specimens with 63% and 60% probabilities. Four specimens of the *S. bicolor* a priori group were assigned to other species: 1 specimen to *S. erecta* with 77% probability (17% to *S. hispida* and 5% to *S. bicolor*; Semple 10732 WAT from Alleghany Co., Virginia), 1 specimen to *S. roanensis* with 61% probability (25% to *S. sciaphila and 122% to S. hispida*; Semple 10656 WAT from Leeds Co., Ontario), 1 specimen to *S. hispida* with 57% probability (39% to *S. bicolor*; Semple 10676 WAT from Greene Co., Pennsylvania), and 1 specimen to *S. sciaphila* with 44% probability (24% to *S. hispida*, 20% to *S. bicolor* and 11% to *S. roanensis*; Semple & Suripto 9839 WAT from Towns Co., Georgia). Fifteen of

the 20 specimens of the *S. sciaphila* a priori group (75%) were assigned a posteriori to the *S. sciaphila* group: 3 specimens with 87% probability, 3 specimens with 73-76% probability, 4 specimen with 60-67% probability, 3 specimens with 57% probability (30% to *S. roanensis*; *Shinners 4706* MIN from Columbia Co., Wisconsin), 54% probability (36% to *S. hispida*; Zager 930907-5 MIN from Houston Co., Minnesota), and 54% probability (23% to *S. roanensis* and 11% to *S. erecta*; *Shinners S-44-627* MIN from Carroll Co., Illinois). Five specimens of the *S. sciaphila* a priori group were assigned a posteriori to the other groups: 1 specimen to *S. erecta* with 64% (19% to *S. hispida* and 10% to *S. sciaphila*, and 6% to *S. bicolor*; *Dunevitz 978* MIN from Winona Co., Minnesota) and 4 specimens to *S roanensis* with 89% probability (10% to *S. sciaphila*; *Tenney 545* MIN from Winona Co., Minnesota; long internodes, few leaves), 71% probability (18% to *S. sciaphila* an 10% to *S. hispida*; *Dunevitz 693* MIN from Winona Co., Minnesota), 53% probability (40% to *S. sciaphila* and 6% to *S. hispida*; Hartley 9002 MIN from Debuque Co., Iowa), and 41% probability (36% to *S. sciaphila* and 22% to *S. hispida*; *Dunevitz 699* MIN from Winona Co., Minnesota). Fourteen of the 19 specimens of the *S. roanensis* a priori group (74%) were assigned a posteriori to the *S. roanensis* group: 1 specimen with 96% probability, 3 specimens with 81-84% probability, 5 specimens with 72-78% probability, 4 specimens with 51-59% probability, and 1 specimen with 47% probability (43% to *S. sciaphila*; *Cook et al. C-557* WAT from Haywood Co., North Carolina). Five specimens of the *S. roanensis* a priori group were assigned a posteriori to other groups: 2 specimens to *S. sciaphila* with 85% probability (13% to *S. roanensis*; *Poindexter 05-1580* BOON from Ashe Co., North Carolina) and 67% probability (30% to *S. roanensis*; *Biltmore Herb. 4622b* NY from Rutherford Co., North Carolina); and 3 specimens to *S. hispida* with 79% probability (212), 62% probability (108), and 52% probability (Boone s.n.4 TAWES from Garrett Co., Maryland). Forty-two of the 76 specimens of the *S. hispida* a priori group (55%) were assigned a posteriori to the *S. hispida* group: 4 specimens with 91-94% probability, 5 specimens with 80-86% probability, 8 specimens with 70-78% probability, 13 specimens with 60-69% probability, 8 specimens with 51-59% probability, and 4 specimens with 38-48% probability). Thirty-four specimens of the *S. hispida* a priori group plus 1 specimen not assigned to an a priori group were assigned a posteriori to other groups: 17 to *S. bicolor* with 83-43% probability, 7 to *S. roanensis* with 91-48% probability, 7 to *S. sciaphila* with 93-36% probability, and 4 to *S. erecta* with 85-69% probability. Two specimens of var. *arnoglossa*, 20 specimens of var. *hispida*, 7 specimens var. *huronensis,* and 5 specimens var. *tonsa* were included among the 34 specimens of *S. hispida* assigned a posteriori to other species.

Two dimensional plots of CAN1 versus CAN3 and CAN1 versus CAN2 canonical scores for 150 specimens of *Solidago bicolor*, *S. erecta*, *S. hispida*, S. *roanensis*, and *S. sciaphila* are presented in Fig. 16. Eigenvalues on the first three axes were 1.148, 0.787 and 0.226.

Table 5. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of four a priori groups; a posteriori placements to groups in rows.

Group	*bicolor*	*erecta*	*hispida*	*roanensis*	*sciaphila*	% correct
bicolor	13	1	1	1	1	76
erecta	0	15	2	0	1	83
hispida	18	4	42	5	7	55
roanensis	0	0	3	14	2	74
sciaphila	0	1	0	4	15	75
Totals	31	21	48	24	26	66

Jackknifed classification matrix

Group	bicolor	erecta	hispida	roanensis	sciaphila	% correct
bicolor	13	1	1	1	1	76
erecta	0	15	2	0	1	83
hispida	18	4	42	5	7	55
roanensis	0	0	3	11	5	58
sciaphila	0	1	0	4	15	75
Totals	31	21	48	21	29	64

Figure 17. Plot of canonical scores (CAN1 vs CAN3 and CAN1 vs CAN2) for 150 specimens of *Solidago* subsect. *Squarrosae*: *S. bicolor* (red circles), *S. erecta* (green ×s, *S. hispida* (black +s), *S. roanensis* (open blue stars), and *S. sciaphila* (pink pentagons).

Three species a priori groups analysis I

In the STEPWISE discriminant analysis of 59 specimens of three species level a priori groups (*S. bicolor*, *S. roanensis*, and *S. sciaphila*), the following six traits were selected as best separating the groups and are listed in order of decreasing F-to-remove values: disc floret pappus length at anthesis (12.42), upper leaf length (11.59), ray floret lamina length (10.53), mid stem leaf width (9.96), number of ray florets (5.66), and involucre height (4.83). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of $p = 0.000$ that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 6. F-values based on Mahalanobis distances between group centroids indicated the largest separation was between *S. bicolor* and *S. sciaphila* (14.769), and the least separation was between *S. roanensis* and *S. sciaphila* (4.640).
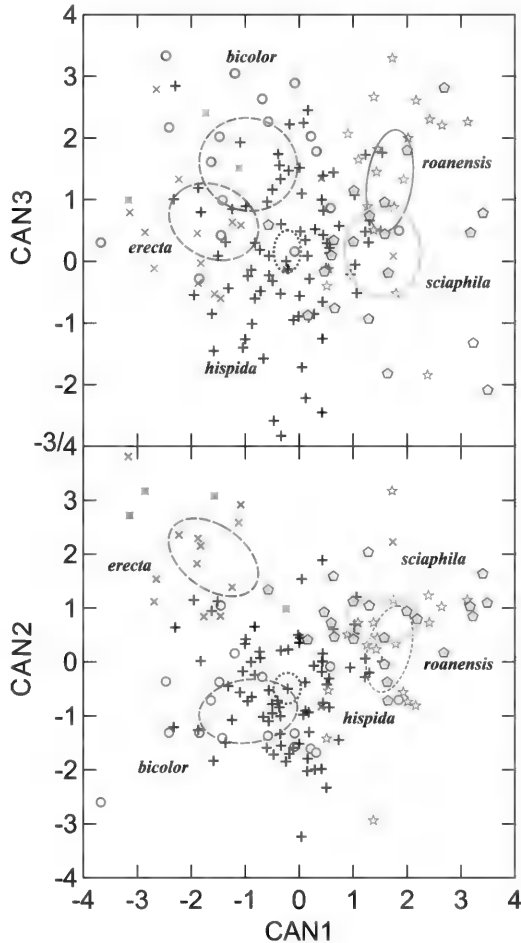
Table 6. Between groups F-matrix for the three a priori groups analysis (df = 6 51).

Group	*bicolor*	*roanensis*
roanensis	7.528	
sciaphila	14.769	4.640

Wilks' lambda = 0.2713 df = 6 2 56; Approx. F= 7.8194 df = 12 102 prob = 0.0000

In the Classificatory Discriminant Analysis of the three species level a priori groups (*S. bicolor*, *S. roanensis*, and *S. sciaphila*), percents of correct a posterori assignment to the same a priori group ranged from 70-88%. The Classification matrix and Jackknife classification matrix are presented in Table 7.   Results are presented in order of decreasing percents of correct placement. Fourteen of 16 specimens of the *S. bicolor* a priori group (88%) were assigned a posteriori to the *S. bicolor* group; 9 specimens with 91-100% probability, 3 specimens with 86-87% probability, and 2 specimens with 79% and 70% probabilities. Two specimens of the *S. bicolor* a priori group plus one not included in an a priori group were assigned a posteriori to *S. roanensis* with 84% probability (16% to *S. sciaphila*; *Hinds* 3826 from Cape Breton, Nova Scotia), 80% probability (15% to *S. bicolor* and 5% to *S. roanensis*; *Semple 10656* WAT from Leeds Co., Ontario), and 61% probability (31% to *S. bicolor* and 5% to *S. roanensis*; *Shchepanek 3788* WAT from Kings Co., Prince Edward Island). Eighteen of the 23 specimens of the *S. sciaphila* a priori group (78%) were assigned a posteriori to the *S. sciaphila* group: 9 specimens with 91-96% probability, 5 specimens with 80-89% probability, 1 specimen with 76% probability; 2 specimens with 65-67% probability, and 1 specimen with 51% probability (49% to *S. roanensis*; *Semple 11851* WAT from Vernon Co., Wisconsin). Five specimens of the *S. sciaphila* a priori group were assigned a posteriori to the other groups: 3 specimens to *S. roanensis* with 90% probability (7% to *S. sciaphila*; *Semple 11854* WAT from Carroll Co., Illinois), 59% probability (41% to *S. sciaphila*; *Semple 11851* WAT from Vernon Co., Wisconsin), and 40% probability (31% to *S. sciaphila* and 29% to *S. bicolor*; *Dunevitz 911* MIN from Winona Co., Minnesota); and 2 specimens to *S. bicolor* with 54% probability (39% to *S. roanensis*; *Dunevitz 699* MIN from Winona Co., Minnesota), and 35% probability (33% to *S. sciaphila* and 32% to *S. roanensis*; *Dunevitz 978* MIN from Winona Co., Minnesota). Fourteen of the 20 specimens of *S. roanensis* a priori group (70%) were assigned a posteriori to the *S. roanensis* group; 3 specimens with 91-97% probability, 2 specimens with 88-89% probability, 3 specimens with 76-77% probability, 2 specimens with 68% and 60% probabilities, 2 specimens with 55% probability (44% to *S. sciaphila,* and 30% to *S. sciaphila* and 14% to *S. bicolor*, respectively), and 1 specimen with 46% probability (36% to *S. bicolor* and 19% to *S. sciaphila*; *Radford 6481* NCU from Macon Co., North Carolina). Six specimens of the *S. roanensis* a priori group were assigned to other species: 4 specimens to *S. sciaphila* with 89% probability (*Biltmore Herb. 4622b* NY from Rutherford Co., North Carolina), 71% probability (*Cusick 25763* NY from Garrett Co., Maryland), 63% probability (*Biltmore Herb. 4622* NY), and 62% probability *(Cook et al. C-557* WAT from Haywood Co., North Carolina); and 2 specimens to *S. bicolor* with 55% probability (39% to *S. roanensis* and 7% to *S. sciaphila*; *Heller & Halbach 1178* NY from Augusta Co., Virginia) and 51% probability (48% to *s. roanensis*; *G. Morton 1747* NY from Giles Co., Virginia).

A two dimensional plot of CAN1 versus CAN2 canonical scores for 59 specimens of *Solidago bicolor*, S. *roanensis*, and S. *sciphila* are presented in Fig. 18. Eigenvalues on the first two axes were 1.7439, and 0.344.

Table 7. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of three a priori groups; a posteriori placements to groups in rows.

Group	*bicolor*	*roanensis*	*sciaphila*	% correct
bicolor	14	2	0	88
roanensis	2	14	4	70
sciaphila	2	3	18	78
Totals	18	19	22	78

Jackknifed classification matrix

Group	*bicolor*	*roanensis*	*sciaphila*	% correct
bicolor	14	2	0	88
roanensis	3	11	6	55
sciaphila	2	5	16	70
Totals	19	18	22	69
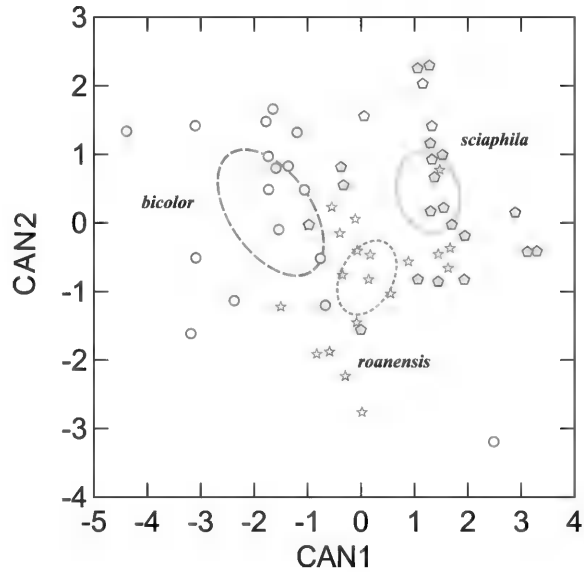
Figure 18. Plot of canonical scores (CAN1 vs CAN2) for 59 specimens of *Solidago* subsect. *Squarrosae*: *S. bicolor* (red circles), *S. roanensis* (open blue stars), and *S. sciaphila* (pink pentagons).

Three species a priori groups analysis II

In the STEPWISE discriminant analysis of 112 specimens of three species level a priori groups (*S. bicolor*, *S. hispida* and *S. roanensis*), the following seven traits were selected as best separating the groups and are listed in order of decreasing F-to-remove values: disc floret pappus length at anthesis (20.21), mid stem leaf length (12.89), number of ray florets (7.66), ray achene body length (4.92), outer phyllary length (4.76), inner phyllary length (4.76), and ray floret lamina width (4.70). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all

groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 8. F-values based on Mahalanobis distances between group centroids indicated the largest separation was between *S. hispida* and *S. roanensis* (11.345), and the least separation was between *S. bicolor* and *S. hispida* (7.716).

Table 8. Between groups F-matrix for the three a priori groups analysis (df = 7   103).

Group	*bicolor*	*hispida*
hispida	7.716	
roanensis	11.226	11.345

Wilks' lambda = 0.3632 df = 7 2 109; Approx. F= 9.7029 df = 14 206 prob = 0.0000

In the Classificatory Discriminant Analysis of the three species level a priori groups (*S. bicolor*, *S. hispida*, and *S. roanensis*), percents of correct a posterori assignment to the same a priori group ranged from 75-84%. The Classification matrix and Jackknife classification matrix are presented in Table 9. Results are presented in order of decreasing percents of correct placement. Sixteen of 19 specimens of the *S. roanensis* a priori group (84%) were assigned a posteriori into the *S. roanensis* group; 13 specimens with 90-100% probability, and 2 specimens with 76% probability. Three specimens of the *S. roanensis* a priori group were assigned to *S. hispida* with 85% probability (14% to *S. roanensis*; *Boon s.n.-4* TAWES from Garrett Co., Maryland), 49% probability (40% to *S. roanensis* and 12% to *S. bicolor*; *Rydberg 8064* NY from Smyth Co., Virginia), and 49% probability (37% to *S. roanensis* and 13% to *S. bicolor*; *Radford 6481* NCU from Macon Co., North Carolina). Fifty-seven of the 76 specimens of the *S. hispida* a priori group (75%) were assigned a posteriori to the *S. hispida* group: 15 specimens with 90-98% probability, 15 specimens with 80-89% probability, 9 specimens with 70-79% probability, 9 specimens with 60-67% probability, 8 specimens with 53-58% probability, and 1 specimen with 45% probability (30% to *S. roanensis* and 24% to *S. bicolor*; *Morton & Venn NA12336* TRT from Northern Peninsula, Newfoundland; var. *arnoglossa*). Nineteen specimens of the *S. hispida* a priori group were assigned a posteriori to the other species: 10 yellow-rayed specimens were assigned a posterior to *S. bicolor* with 84% probability (12% to *S. hispida*; *Semple et al. 2987* WAT from Scioto Co., Ohio; sparsely very short strigose lower stem, moderately so in inflorescence), 81% probability (19% to *S. hispida*; *Semple & Brouillet 3638* WAT from Greene Co., New York), 79% probability (20% to *S. hispida*; *Morton NA6751a* TRT from Manitoulin Dist., Ontario), 71% probability (24% to *S. hispida*; *Oldham 37024* from Cochrane Dist., Ontario; var. aff. *huronensis*), 70% probability (30% to *S. hispida*; *Hall 693 AE-AF* MT from Thetford Mines, Québec), 65% probability (22% to *S. hispida* and 13% to *S. roanensis*; *Morton NA3978* WAT from Gaspésie, Québec), 64% probability (35% *S. hispida*; *Hall 829 DF* MT from Kingsbury, Québec), 64% probability (36% *S.* hispida; *Semple & B. Semple 11426* WAT from Gaspésie, Québec), 63% probability (26% *S. hispida* and 10% *S. arnoglossa*; *Cook & Tereszchuk C-156* WAT from Coos Co., New Hampshire), and 56% probability (44% to *S.hispida*; *Morton NA6656* TRT from Manitoulin Dist., Ontario); and 10 specimens including one added to the a posteriori sample were assigned a posterior to *S. roanensis* with 95% probability (*Morton & Venn NA12186* WAT from Table Mt., Newfoundland; var. *tonsa*), 75% probability (*Morton & Venn NA12186* TRT from Table Mt., Newfoundland; var. *tonsa*), 70% probability (29% to *S. hispida*; *Bakowsky s.n.* WAT from Lambton Co., Ontario; var. *huronensis*), 67% probability (33% to *S. hispida*; *Bakowsky s.n.* WAT from Lambton Co., Ontario; var. *huronensis*), 64% probability (25% to *S. hispida* and 11% to *S. bicolor*;

Morton & Venn NA12474 TRT from Blow-me-down Mts., Newfoundland; var. *arnoglossa*), 60% probability (21% to *S. bicolor* and 19% to *S. hispida*; *Morton & Venn NA12186* WAT from Table Mt., Newfoundland; var. *tonsa*), 60% probability (30% to *S. hispida* and 10% to *S. bicolor*; *Morton NA4086* TRT from the Gaspé, Québec; var. *tonsa*), 56% probability (44% to *S. hispida*; *Morton & Venn NA12438* TRT from Newfoundland, var. *tonsa*), and 52% probability (47% to *S. hispida*; *Bakowsky s.n.* WAT from Lambton Co., Ontario; var. *huronensis*). Twelve of the 17 specimens of *S. bicolor* a priori group (71%) were assigned a posteriori to the *S. bicolor* group; 5 specimens with 94-100% probability, 4 specimens with 82-88% probability, and 3 specimens with 74-78% probability. Five specimens of the *S. bicolor* a priori group were assigned to the other species: 1 specimen to *S. roanensis* with 96% probability (*Semple 10656* WAT from Leeds Co., Ontario); and 4 specimens to *S. hispida* with 68% probability (20% to *S. bicolor* and 13% to *S. roanensis*; *Shchepanek 3788* WAT from Kings Co., Prince Edward Island), 57% probability (43% to *S. bicolor*; *Semple & Keir 4797* WAT from Halifax Co., Nova Scotia), 57% probability (42% to *S. bicolor*; *Semple 10676* WAT from Greene Co., Pennsylvania), and 52% probability (47% to S. bicolor; *Oldham 22125* WAT from the Magdalen Is., Québec).

Table 9. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of three a priori groups; a posteriori placements to groups in rows.

Group	bicolor	hispida	roanensis	% correct
bicolor	12	4	1	71
hispida	10	57	9	75
roanensis	0	3	16	84
Totals	22	64	26	76

Jackknifed classification matrix

Group	bicolor	hispida	roanensis	% correct
bicolor	11	5	1	65
hispida	10	57	9	75
roanensis	1	3	15	79
Totals	22	65	25	74

A two dimensional plot of CAN1 versus CAN2 canonical scores for 112 specimens of *Solidago bicolor*, *S. hispida*, and, S. *roanensis* is presented in Fig. 19. Eigenvalues on the first two axes were 0.830 and 0.505.

Three species groups analysis III

In the STEPWISE discriminant analysis of 85 specimens of three species level a priori groups (*S. hispida*, *S. sciaphila* and *S. speciosa*), the following seven traits were selected as best separating the groups and are listed in order of decreasing F-to-remove values: disc floret pappus length at anthesis (33.15), number of ray florets (13.07), outer phyllary length (13.34), mid stem leaf length (10.31), ray floret lamina length (9.72), disc corolla length (7.80), and inner phyllary length (4.50). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of $p = 0.000$ that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 10.   F-values based on Mahalanobis
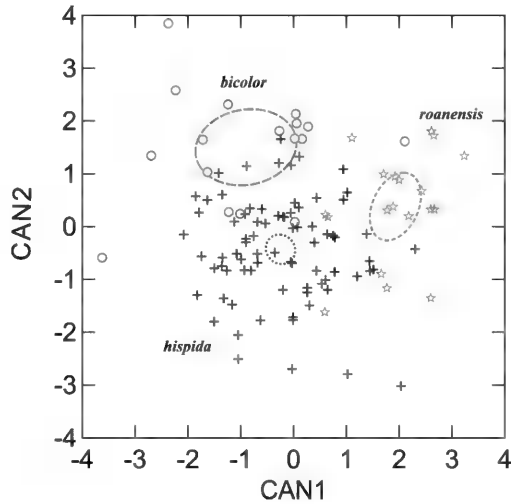
Figure 19. Plot of canonical scores (CAN1 vs CAN2) for 112 specimens of *Solidago* subsect. *Squarrosae*: *S. bicolor* (red circles), *S. hispida* (black +s), and *S. roanensis* (open blue stars).

distances between group centroids indicated the largest separation was between *S. hispida* and *S. speciosa* (29.367), and the least separation was between *S. hispida* and *S. sciaphila* (13.014).

Table 10. Between groups F-matrix for the three a priori groups analysis (df = 7 76).

Group	hispida	sciaphila
sciaphila	13.014	
speciosa	29.367	22.687

Wilks' lambda = 0.1199 df = 7 2 82; Approx. F= 20.4951 df = 14 152 prob = 0.0000

In the Classificatory Discriminant Analysis of the three species level a priori groups (*S. hispida*, *S. sciaphila* and *S. speciosa*), percents of correct a posterori assignment to the same a priori group ranged from 90-96%.   The Classification matrix and Jackknife classification matrix are presented in Table 11.   Results are presented in order of decreasing percents of correct placement. Twenty-two of 23 specimens of the *S. speciosa* a priori group (96%) were assigned a posteriori into the *S. speciosa* group; 18 specimens with 91-100% probability (13 with 100%), 2 specimens with 86% probability, and 1 specimen with 73% probability (27% to *S. sciaphila*).   One specimen of the *S. speciosa* a priori group was assigned to *S. hispida* with 71% probability (29% to *S. speciosa*; *Semple & Chmielewski 6103* WAT from Lancaster Co., South Carolina; a 177 cm tall plant with mostly wilted lower stem leaves).   Nineteen of the 20 specimens of the *S. sciaphila* a priori group (95%) were assigned a posteriori to the *S. sciaphila* group: 16 specimens with 90-100% probability, and 2 specimens with 83% probability, and 1 specimen with 46% probability (31% to *S. speciosa* and 23% to *S. hispida*; *Zager 930907-5* MIN from Houston Co, Minnesota; a 52 cm shoot with serrate lower and mid stem leaves and entire upper stem leaves).   One specimen of the *S. sciaphila* a priori group

was assigned a posteriori to *S. speciosa* with 62% probability (27% to *S. sciaphila* and 11% to *S. hispida*; *Dunevitz 978* MIN from Winona Co. Minnesota; a 74 cm tall shoot with serrate large basal rosette and lower stem leaves and entire mid and much reduced upper stem leaves).   Thirty-eight of the 42 specimens of *S. hispida* a priori group (75%) were assigned a posteriori to the *S. hispida* group (40 var. *hispida* and 2 var. *huronensis*); 32 specimens with 91-100% probability, 3 specimens with 81-89% probability, 1 specimen with 73% probability, and 2 specimens with 69% probability (17% to *S. sciaphila* and 14% to *S. speciosa*) and 62% (38% to *S. sciaphila*). Four specimens of the *S. hispida* a priori group were assigned to the other species: 3 specimens to *S. sciaphila* with 98% probability (2% to *S. hispida*; *Morton & Venn NA7682* WAT from Bruce Co., Ontario; a tall var. *huronensis* plant with glabrate stem), 98% probability (2% to *S. hispida*; *Hamel C68020* MT from the eastern townships of Québec; a 34 cm tall shoot with densely woolly stem), and 58% probability (41% to *S. hispida*; *Semple 9076* WAT from Douglas, Wisconsin; a 48 cm tall shoot with moderately hispid-villous stem and small mid and upper stem leaves); and 1 specimen to *S. speciosa* with 60% probability (35% to *S. hispida* and 5% to *S. sciaphila*; Morton *NA6656* WAT from Georgian Bay, Manitoulin Dist., Ontario).

Table 11. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of three a priori groups; a posteriori placements to groups in rows.

Group	*hispida*	*sciaphila*	*speciosa*	% correct
hispida	38	3	1	90
sciaphila	0	19	1	95
speciosa	1	0	22	96
Totals	39	22	24	93

Jackknifed classification matrix

Group	*hispida*	*sciaphila*	*speciosa*	% correct
hispida	38	3	1	91
sciaphila	0	18	2	90
speciosa	1	0	22	96
Totals	40	21	25	92

A two dimensional plot of CAN1 versus CAN2 canonical scores for 86 specimens of *Solidago hispida*, *S. sciaphila* and *S. speciosa* is presented in Fig. 20. Eigenvalues on the first two axes were 2.813 and 1.187.

Two species a priori groups analysis of *Solidago hispida* and *S. bicolor*
In the STEPWISE discriminant analysis of 93 specimens of *S. bicolor* and *S. hispida*, the following four traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: upper leaf width (19.12), disc floret pappus length at anthesis (18.70), inner phyllary length (18.05), and ray floret lamina length (8.93). The number of ray florets had the lowest F-to-remove value (0.07). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. *Solidago bicolor* and *S. hispida* had an F-to separate value of 12.602 (Wilks' lambda = 0.6175 df = 4 1 91; Approx. F= 13.6296 df = 4 88 prob. 0.0000).
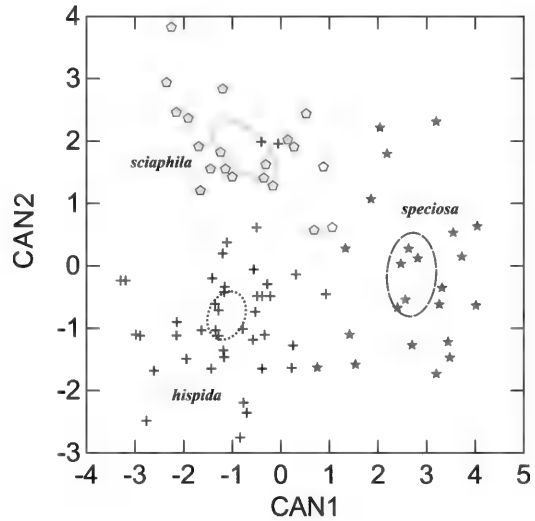
Figure 20. Plot of canonical scores (CAN1 vs CAN2) for 85 specimens of *Solidago hispida* (black +s), *S. sciaphila* (pink pentagons), and *S. speciosa* (yellow stars).

In the Classificatory Discriminant Analysis of the two species level a priori groups, percents of correct a posterori assignment to the same a priori group were 88% for *S. bicolor* and 82% for *S. hispida*. Fifteen of the 17 specimens of *S. bicolor* were assigned a posteriori to *S. bicolor*: 10 specimens with 91-99% probability, 2 specimens with 81-82% probability, 1 specimen with 78% probability, and 1 specimen with 65% probability. Two specimens of the *S. bicolor* a priori group with white rays were assigned to *S. hispida*: with 79% probability (*Semple 10676* WAT from Greene Co., Pennsylvania) and 66% probability (*Shchepanek 3788* WAT from Kings Co., Prince Edward Island). Sixty-two of the 76 specimens of *S. hispida* were assigned a posteriori to the *S. hispida* group: 40 specimens with 90-100% probability, 9 specimens with 80-89% probability, 5 specimens with 73-79% probability, 1 specimen with 64% probability, and 7 specimens with 51-59% probability. Fourteen specimens of the *S. hispida* a priori group with yellow rays were assigned a posteriori to *S. bicolor*: 5 specimens with 80-89% probability, 1 specimen with 72% probability, 5 specimens with 65-69% probability, and 2 with 56% and 55% probabilities.
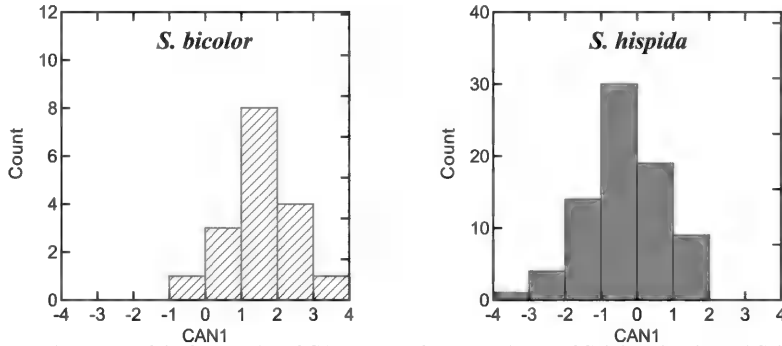
Frequencies of CAN1 canonical scores for 93 specimens of *S. bicolor* and *S. hispida* are presented in histograms in Fig. 21. The Eigenvalue on the first axis was 0.620.

Table 12. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of two a priori groups; a posteriori placements to groups in rows.

Group	*bicolor*	*hispida*	% correct
bicolor	15	2	88
hispida	14	62	82
Totals	29	64	83

Jackknifed classification matrix

Group	bicolor	hispida	% correct
bicolor	14	3	82
hispida	15	61	80
Totals	29	64	81

Figure 20. Histograms of the frequencies of CAN1 scores for 93 specimens of *Solidago bicolor* and *S. hispida*.

Four variety level a priori groups analysis of *Solidago hispida* I

In the STEPWISE discriminant analysis not including stem height of 76 specimens of four varietal level a priori groups in *S. hispida* (*var. arnoglossa*, var. *hispida*, var. *huronensis*, and var. *tonsa*), the following three traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: outer phyllary length (14.87), number of ray florets (11.57), and disc floret pappus length at anthesis (9.62). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 13. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between var. *hispida* and var. *tonsa* (18.503); the smallest separation was between var. *arnoglossa* and var. *hispida* (7.542).

Table 13. Between groups F-matrix for the four variety level a priori groups analysis of *S. hispida* (df = 3   70).

Group	arnoglossa	hispida	huronensis
hispida	9.715		
huronensis	12.750	10.063	
tonsa	7.542	18.5037	8.869

Wilks' lambda = 0.3189 df = 3 3 72; Approx. F= 11.3220 df = 9 170 prob = 0.0000

In the Classificatory Discriminant Analysis not including stem height of the four varietal level a priori groups in *S. hispida* (*var. arnoglossa*, var. *hispida*, var. *huronensis*, and var. *tonsa*),

percents of correct a posterori assignment to the same a priori group ranged from 50-89%. The Classification matrix and Jackknife classification matrix are presented in Table 14. Results are presented in order of decreasing percents of correct placement. Eight of the 9 specimens of the var. *tonsa* a priori group (89%) were assigned a posteriori into the var. *tonsa* group; 4 specimens with 94-100% probability, 1 specimen with 87% probability, 1 specimen with 60% probability, 1 specimen with 55% probability (28% to var. *huronensis*, 9% to var. *arnoglossa*, and 8% to var. *hispida*; 186), and 2 specimens with 48% probability (*Morton NA4086* TRT from the Gaspé, Québec) and 40% probability (*Morton & Venn NA12186* TRT from Table Mt., Newfoundland). One specimen of the var. *tonsa* a priori group was assigned a posteriori to var. *huronensis* with 51% probability (24% to var. *hispida* and 22% to var. *tonsa*; *Morton & Venn NA12186* WAT from Table Mt., Newfoundland). Thirty of the 40 specimens of var. *hispida* a priori group (75%) were assigned a posteriori to the var. *hispida* group; 4 specimens with 90-93% probability, 7 specimens with 82-88% probability, 5 specimens with 70-79% probability, 5 specimens with 61-69% probability, 5 specimens with 56% probability (41% to var. *arnoglossa*; Hamel *C66206* MT from Thetford Mines, Québec), 56% probability (34% to var. *huronensis*, 5% to var. *arnoglossa*; *Morton NA3978* WAT from Bic Is., Gaspé, Québec), 54% probability (34% to var. *huronensis* and 11% to var. *arnoglossa*; *Baldwin 11554* WAT from Manitoba), 54% probability (35% to var. *arnoglossa*, 10% to var. *huronensis*; *Semple & B. Semple 6723* WAT from Kenora Dist., Ontario), and 53% probability (24% to var. *huronensis* and 22% to var. *arnoglossa*; *Semple & Bramall 2868* WAT from Algoma Dist., Ontario); and 4 specimens with 46% probability (44% to var. *huronensis*; *Doucet Do-59-7-3* MT from N of Coleraine, Québec), 46% probability (29% to var. *huronensis*, 13% to var. *arnoglossa*, and 13% to var. *tonsa*; *Hall 195 F* MT from Parq du Mont-Orford, Québec), 41% probability (41% to var. *arnoglossa* and 15% to var. *tonsa*; *Hall 795 BE* MT from St-Joseph-de-Coleraine Réserve écologique, Québec), and 32% probability (30% to var. *huronensis*, 26% to var. *arnoglossa*, and 12% to var. *tonsa*; *Doucet Do-59-7-5* MT from Black Lake, Québec; moderately densely woolly stem). Thirteen specimens of the var. *hispida* a priori group were assigned to other varieties: 7 specimens to var. *arnoglossa* with 79% probability (13% to var. *hispida* and 7% to var. *tonsa*; *Semple & Brammall 2818* WAT from Cochrane Dist., Ontario), 76% probability (20% to var. *hispida*; *Doucet Do-59-7-6* MT from Black Lake, Québec), 74% probability (16% to var. *hispida*; *Semple & Heard 8315* WAT from Fulton Co., Arkansas), 56% probability (31% to var. *hispida*; and 13% to var. *tonsa*; *Semple & Brammall 2846* from Sudbury Dist., Ontario), 50% probability (34% to var. *hispida* and 10% to var. *tonsa*; *Sauleda 4285* WAT from Rappahannock Co., Virginia), 49% probability (47% to var. *hispida*; *Semple & Brouillet 3638* WAT from Greene Co., New York), and 34% probability (34% to var. *tonsa*, 22% to var. *hispida* and 10% to var. *huronensis*; *Hall 5824 AI* MT from N of lac La Rauche, Québec); 5 specimens to var. *huronensis* with 85% probability (13% to var. *hispida*; *Semple 9076* WAT from Douglas Co., Wisconsin), 82% probability (16% to var. *hispida*; *Arnett & Hastings 1081* LSU from Rapides Par., Louisiana; moderately hispid-woolly stem), 78% probability (13% to var. *tonsa*; *Hamel C68020* MT from canton de Nelson, Québec), 66% probability (33% to var. *hispida*; *Semple & Suripto 9914* WAT from Oregon Co., Missouri), and 65% probability (25% to var. *tonsa* and 7% to var. *hispida*; *Thomas et al. 69272* WAT from Ashley Co., Arkansas; moderately dense long woolly hairs on stem); and 1 specimen to var. *tonsa* with 91% probability (7% to var. *arnoglossa*; *Morton & Venn NA12163* TRT from Gros Morne N.P., Newfoundland). Eight of the 11 specimens of the var. *huronensis* a priori group (73%) were assigned a posteriori to the var. *huronensis* group: 4 specimens with 93-96% probability, 1 specimen with 83% probability, 1 specimen with 62% probability, and 2 specimens with 57% probability (40% to var. *tonsa*; *Bakowsky s.n.* WAT from Lambton Co., Ontario) and 52% probability (24% var. *arnoglossa* and 17% var. *hispida*; *Morton & Venn NA7682* WAT from Bruce Co., Ontario). Three specimens of the var.

huronensis group were assigned a posteriori to the var. *hispida* group with 75% probability (18% to var. *huronensis* and 6% to var. *arnoglossa*; *Bakowsky s.n.* WAT from Lambton Co., Ontario), 71% probability (24% to var. *arnoglossa*; *Oldham 37024* WAT from Cockrane Dist., Ontario), and 61% probability (34% to var. *huronensis*; *Bakowsky s.n.* WAT from Lambton Co., Ontario). Eight of 16 specimens of the var. *arnoglossa* a priori groups (50%) were assigned a posteriori to the var. *arnoglossa* group: 3 specimens with 93-97% probability, 1 specimen with 89% probability, 3 specimens with 71-77% probability, and 1 specimen with 66% probability. Eight specimens of the var. *arnoglossa* a priori group were assigned a posteriori to other varieties: 4 specimens to var. *hispida* with 84% probability (9% to var. *arnoglossa* and 7% to var. *huronensis*; *Morton & Venn* NA15322 TRT from Mistassini, Québec), 64% probability (19% to var. *huronensis* and 16% to var. *hispida*; *Morton* NA3978 TRT from Bic Is., Gaspé, Québec), 60% probability (33% to var. *arnoglossa*; *Morton & Venn* NA15322 TRT from Mistassini, Québec), and 52% probability (42% to var. *arnoglossa*; Morton s.n. TRT from Cap au Renaud, Gaspé, Québec); and 2 specimens to var. *huronensis* with 50% probability (23% to var. *hispida*, 19% to var. *tonsa*, and 9% to var. *arnoglossa*; *Morton & Venn NA12474* TRT from Blow-me-down Mts., Newfoundland; moderately woolly stem) and, 44% probability (25% to var. *tonsa*, 17% to var. *hispida*, and 14% to var. *arnoglossa*; *Morton s.n.* TRT

Table 14. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of four variety level a priori groups in *S. hispida*; a posteriori placements to groups in rows.

Group	*arnoglossa*	*hispida*	*huronensis*	*tonsa*	% correct
arnoglossa	8	4	2	2	50
hispida	6	30	3	1	75
huronensis	0	3	8	0	73
tonsa	0	0	1	8	89
Totals	14	37	14	11	71

Jackknifed classification matrix

Group	*arnoglossa*	*hispida*	*huronensis*	*tonsa*	% correct
arnoglossa	8	4	2	2	50
hispida	7	29	3	1	73
huronensis	0	3	7	1	64
tonsa	1	0	1	7	78
Totals	16	36	13	11	67

from Bon Ami Pt., Gaspé. Québec; moderately hispid-woolly stem); and 2 specimens to var. *tonsa* with 42% probability (38% to var. *arnoglossa*,and 16% to var. huronensis; *Morton & Venn NA12336* TRT from the Northern Peninsula, Newfoundland; stem moderately densely woolly) and 40% probability (27% to var. *huronensis*, 20% to var. *arnoglossa*, and 12% to var. *hispida*; *Morton s.n.* TRT from Bon Ami Pt., Gaspé. Québec; moderately hispid-woolly stem).

Two dimensional plots of CAN1 versus CAN3 and CAN1 versus CAN2 canonical scores for 77 specimens of *var. arnoglossa*, var. *hispida*, var. *huronensis*, and var. *tonsa* of *S. hispida* are presented in Fig. 21. Eigenvalues on the first three axes were 0.888, 0.594 and 0.075.
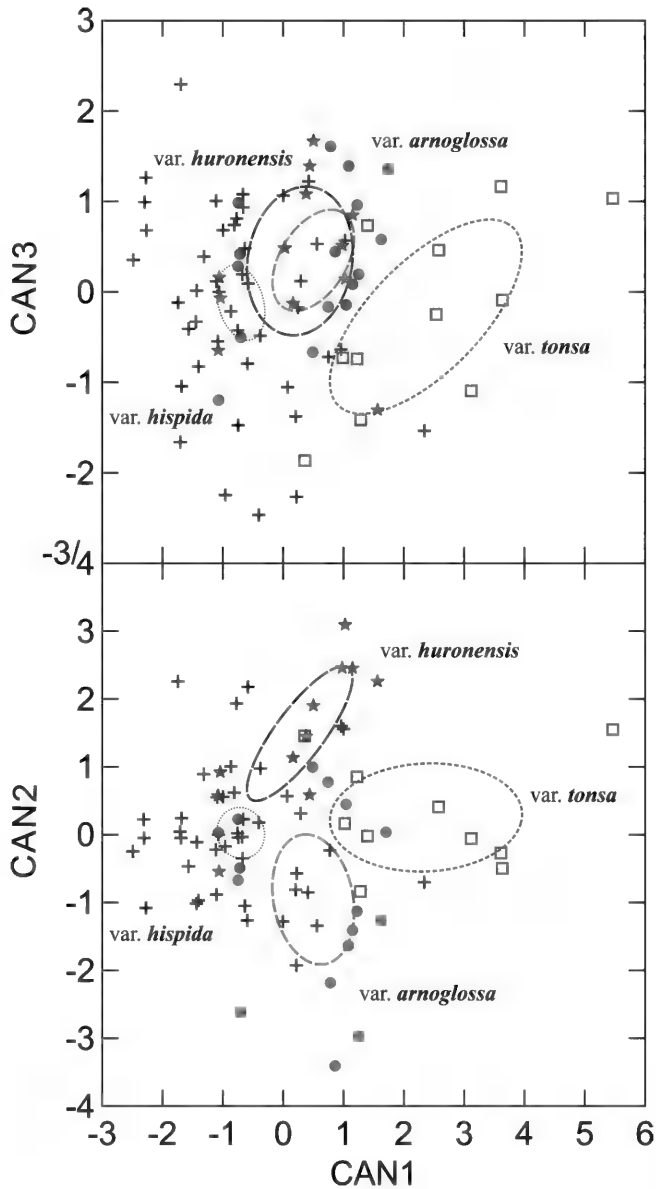
Figure 21. Plot of canonical scores (CAN1 vs CAN3 and CAN1 vs CAN2) for 74 specimens of *Solidago hispida*, stem height not included in analysis: *var. arnoglossa* (red dots), var. *hispida* (black +s), var. *huronensis* (yellow stars), and *var. tonsa* (open blue squares).

Four variety level a priori groups analysis of *Solidago hispida* II

In the STEPWISE discriminant analysis including stem height of 74 specimens of four varietal level a priori groups in *S. hispida* (*var. arnoglossa*, var. *hispida*, var. *huronensis*, and var. *tonsa*), the following five traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: stem height (16.54), number of ray florets (10.75), outer phyllary length (9.17), disc floret pappus length at anthesis (7.17), and mid stem leaf length (3.34). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 15. F-values based on Mahalanobis distances of the between group centroids indicated the largest separations were between var. *hispida* and var. *tonsa* (19.191) and var. *arnoglossa* and var. *hispida* (17.485); the smallest separations were between var. *arnoglossa* and var. *tonsa* (5.666) and var. *hispida* and var. *huronensis* (7.070).

Table 15. Between groups F-matrix for the four a priori group analysis of *S. hispida*, stem height included in the analysis (df = 4 67).

Group	*arnoglossa*	*hispida*	*huronensis*
hispida	17.485		
huronensis	15.257	7.070	
tonsa	5.666	9.191	10.803

Wilks' lambda = 0.2080 df = 4   3   70; Approx. F= 11.9533 df = 12   177   prob = 0.0000

In the Classificatory Discriminant Analysis including stem height of the four varietal level a priori groups in *S. hispida* (*var. arnoglossa*, var. *hispida*, var. *huronensis*, and var. *tonsa*), percents of correct a posterori assignment to the same a priori group ranged from 70-89%. The Classification matrix and Jackknife classification matrix are presented in Table 16. Results are presented in order of decreasing percents of correct placement. Eight of the 9 specimens of the var. *tonsa* a priori group (89%) were assigned a posteriori to the var. *tonsa* group; 5 specimens with 93-100% probability, 1 specimen with 74% probability, 2 specimens with 67% and 64% probabilities, 1 specimen with 51% probability (20% to var. *arnoglossa* 16% to var. *hispida* and 12% to var. *huronensis*; *Morton & Venn NA12186* WAT from Table Mt., Newfoundland).   One specimen of the var. *tonsa* a priori group was assigned a posteriori to var. *arnoglossa* with 53% (46% to var. *tonsa*; *Morton & Venn NA12186* WAT from Table Mt., Newfoundland). Thirty-three of the 39 specimens of var. *hispida* a priori group (85%) were assigned a posteriori to the var. *hispida* group; 14 specimens with 90-99% probability, 6 specimens with 81-86% probability, 4 specimens with 70-79% probability, 1 specimen with 66% probability, and 6 specimens with 58% probability (41% to var. *huronensis*; *Boldwin 11554* WAT from Manitoba), 54% probability (26% to var. *huronensis*, 11% to var. *tonsa*, and 9% to var. *arnoglossa*; *Hall 195 F* MT from Parq du Mont-Orford, Québec), 53% (20% to var. *huronensis*, 16% to var. *tonsa*, and 12% to var. *arnoglossa*; *Hall 5824 AI* MT from N of lac La Rauche, Québec), 53% probability (44% to var. *huronensis*; *Doucet Do-59-7-3* MT from N of Coleraine, Québec), 51% probability (45% to var. *huronensis*; *Doucet Do-59-7-5* MT from Black Lake, Québec; moderately densely woolly stem), and 49% (32% to var. *arnoglossa* and 16% to var. *tonsa*; *Hall 795 BE* MT from St-Joseph-de-Coleraine Réserve écologique, Québec). Nine specimens of the var. *hispida* a priori group were assigned to other varieties groups: 5 specimens to var. *huronensis* with 91%

probability (9% to var. *hispida*; *Thomas et al 69272* WAT from Ashley Co., Arkansas), 87% probability (13% to var. *hispida*; *Arnett & Hastings 1081* LSU from Rapides Par., Louisiana), 86% probability (14% to var. *hispida*; *Semple 9076* WAT from Douglas Co., Wisconsin), 86% probability (6% to var. *hispida* and 6% var. *tonsa*; *Hamel C68020* MT from canton de Nelson, Québec), and 65% probability (35% to var. *hispida*; *Semple & Suripto 9914* WAT from Oregon Co., Missouri); 3 specimens to var. *arnoglossa* with 82% probability (10% to var. *hispida* and 4% to var. *huronensis*; *Semple & Brammall 2868* WAT from Algoma Dist., Ontario), 77% probability (14% to var. *hispida* and 7% to var. *tonsa*; *Semple & Brammall 2818* WAT from Cochrane Dist., Ontario), and 73% probability (17% to var. *hispida* and 6% to var. *huronensis*; *Semple & Keir 4659* WAT from Aroostock Co., Maine). Twelve of 16 specimens of the var. *arnoglossa* a priori groups (75%) were assigned a posteriori to the var. *arnoglossa* group: 5 specimens with 93-98% probability, 3 specimens with 81-86% probabilities, 1 specimen with 71% probability, 2 specimens with 59% probability (37% to var. *hispida* and 4% to var. *huronensis*; *Morton s.n.* TRT from Cap au Renaud, Gaspé, Québec) and 56% probability (35% var. *hispida* and 7% to var. *tonsa*; *Morton & Venn NA15322* TRT from Mistassini, Québec), and 1 specimen with 47% probability (46% to var. *tonsa*; *Morton & Venn NA12336* TRT from Northern Peninsula, Newfoundland). Four specimens of the var. *arnoglossa* a priori group were assigned a posteriori to other varieties: 2 specimens to var. *tonsa* with 57% (28% to var. *arnoglossa* and 9% to var. *huronensis*; *Morton s.n.* TRT from Pt. Bon Ami, Gaspé, Québec) and 48% (27% to var. *arnoglossa*, 16% to var. *huronensis* and 9% to var. *hispida*; *Morton s.n.* TRT from Pt. Bon Ami, Gaspé, Québec); 1 specimen to var. *hispida* with 71% (20% to var. *huronensis* and 8% to var. *arnoglossa*; *Morton NA3978* TRT from Bic Island, Gaspé, Québec), and 1 specimen to var. *huronensis* with 54% (31% var. *hispida* 11% var. *tonsa*; *Morton & Venn NA12474* TRT from Blow-me-down Mts., Newfoundland). Seven of 10 specimens of var. *huronensis* a priori group (70%) assigned a posteriori to the var. *huronensis* group: 4 specimens with 97-98% probability, 1 specimen with 86% probability, 1 specimen with 77% probability, and 1 specimen with 55% probability (43% to var. *tonsa*; *Bakowsky s.n.* WAT from Lambton Co., Ontario). Three specimens of the var. *huronensis* group were assigned a posteriori to the var. *hispida* group with 93% probability (7% to var. *huronensis*; *Oldham 37024* WAT from Cockrane Dist., Ontario), 80% probability (16% to var. *huronensis*; *Bakowsky s.n.* WAT from Lambton Co., Ontario), and 65% probability (34% to var. *huronensis*; *Bakowsky s.n.* WAT from Lambton Co., Ontario). Two dimensional plots of CAN1 versus CAN3 and CAN1 versus CAN2 canonical scores for 75 specimens of *var. arnoglossa*, var. *hispida*, var. *huronensis*, and var. *tonsa* of *S. hispida* are presented in Fig. 22. Eigenvalues on the first three axes were 1.659, 0.630, and 0.110.

Table 16. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of four varietal a priori groups in *S. hispida,* stem height included in the analysis; a posteriori placements to groups in rows.

Group	arnoglossa	hispida	huronensis	tonsa	% correct
arnoglossa	12	1	1	2	75
hispida	2	33	3	1	85
huronensis	0	3	7	0	70
tonsa	1	0	0	8	89
Totals	15	37	11	11	81

Jackknifed classification matrix

Group	*arnoglossa*	*hispida*	*huronensis*	*tonsa*	**% correct**
arnoglossa	10	2	1	3	63
hispida	3	33	3	1	83
huronensis	0	3	6	1	60
tonsa	1	0	0	8	89
Totals	34	38	10	13	77

DISCUSSION

Species level analyses

The results of the six species level multivariate analyses indicate that *Solidago bicolor*, *S. erecta*, *S. hispida*, *S. porteri*, *S. roanensis*, and *S. sciaphila* are distinct species. While the six species are for the most part morphologically similar, each has a diagnostic set of traits distinguishing it from the other five species. When traits often used in keys (e.g., ray floret color, stem hair density and distribution, and numbers of veins on the phyllaries) but not included in the analyses were considered, then most of the specimens that had been assigned a posteriori to a different group than each was assigned to a priori were easily assigned to their a priori groups. For example, all of the specimens of *S. bicolor* specimens had white rays even though some were assigned to other species using just the technical leaf and floral traits. All the specimens of *S. roanensis* had lower stems without hairs and increasingly more densely hairy stems distally, and most had multi-veined phyllaries but not all. There is considerable overlap in ranges of trait values among the species which resulted in a posterior miss assignments in the analyses that are not likely to happen using diagnostic traits not included in the analyses.

The results of the first analysis demonstrate that *Solidago porteri* has traits that strongly separate it from the other species. All specimens of *S. porteri* were assigned a posteriori to *S. porteri* with 96-100% probability. Difficulty in recognizing the species in the past has come mainly from lack of experience with the species because very few collections have been made by very few people. *Solidago porteri* is the only hexaploid taxon in *S.* subsect. *Squarrosae* (Semple and Estes 2014) and is most similar to species that are only known at the diploid level. The results of the multivariate study provide very little evidence as to which species (singular or plural) *S. porteri* is most closely related. In Fig. 17, symbols for specimens of *S. erecta* are closer to those of *S. porteri* on the CAN1 versus CAN2 plot, but symbols for the two species were strongly separated on the CAN1 versus CAN3 plot. Whether *S. porteri* is of allopolyploid origins or simply the result of autoploidy within a species that once included diploids and tetraploids cannot be resolved on the basis of morphology. Cronquist (1980) discussed the species known only at the time from the type collection under *S. hispida*.

The results of the five species analysis support the recognition of *Solidago bicolor*, *S. erecta*, *S. hispida*, *S. roanensis*, and *S. sciaphila* as separate species. Symbols for *S. erecta* were nearly fully separated from symbols for other species in the CAN1 versus CAN2 plot in Fig. 17 and the 95% confidence ellipse was well separated from the confidence ellipses for the other species. Based on F values between group centroids, *S. bicolor* and *S. hispida* (5.328) and *S. roanensis* and *S. sciaphila* (3.110) are the two most similar pairs of species, at least in terms of the traits selected to separate taxa in the five species analysis. Symbols for *S. bicolor* and *S. hispida* were mostly separated from symbols for *S. roanensis* and *S. sciaphila* in the CAN1 versus CAN2 diagram, but the confidence limits for the latter two species overlapped on these two axes much more than they did on the CAN1 versus CAN3 axes. Diagnostic differences in stem indument density and distribution and number of veins on the phyllaries were not included as traits in the analyses. When these traits are included then
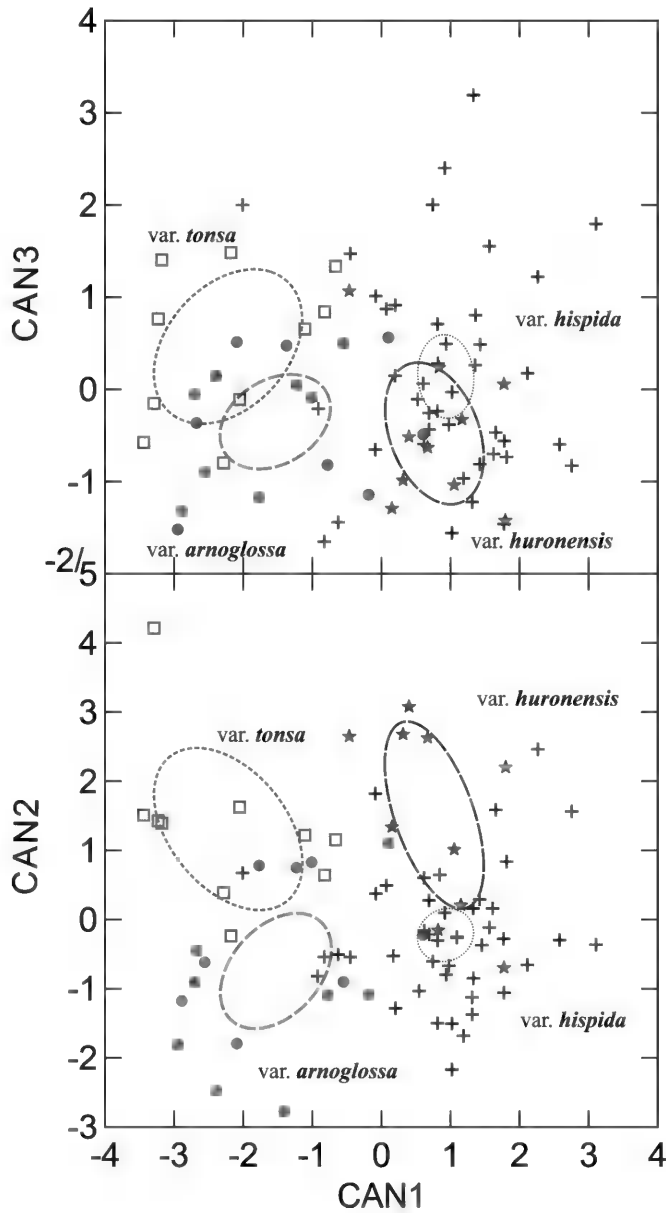
Figure 22. Plot of canonical scores (CAN1 vs CAN3 and CAN1 vs CAN2) for 75 specimens of *Solidago hispida*, stem height included in the analysis: *var. arnoglossa* (red dots), var. *hispida* (black +s), var. *huronensis* (yellow stars), and *var. tonsa* (open blue squares).

S. roanensis and *S. sciaphila* are much easier to distinguish. The ranges of the two species are fully allopatric; both species occur in Illinois but *S. roanensis* is confined to the southern areas of the state while *S. sciaphila* occurs only in the northwestern corner of the state. Neither occurs in the flat prairies portion of Illinois.

The glabrous lower and mid stems of *Solidago erecta* usually make the species easily distinguished from the other species in the *S. bicolor* complex. The glabrous and glabrate stem varieties of *S. hispida* occur north or the range of *S. erecta.* Lower and mid stems of *S. erecta* are hairless while some hairs occur on stems and peduncles in the inflorescence. Mid and upper stems of *S. roanensis* are much hairier than those of *S erecta*, which is more likely to be confused with diploid plants of *S. speciosa* than with plants of the *S. bicolor* group of species. *Solidago erecta* usually has smaller leaves and shorter stems than *S. speciosa*, and large inflorescences of the former are more open and have shorter branches than the latter. Stem height in *Solidago* is a plastic trait greatly influenced by growing conditions. The field experience of the first author over many years indicates that when *S. speciosa* and *S. erecta* occur together, the smaller plants are always *S. erecta*.

The obvious field character difference between white rayed *Solidago bicolor* and yellow rayed *S. hispida* is not always discernable on herbarium specimens, particularly those that are old or were collected with heads past blooming. Plants of the two species collected in fruit can be challenging to place to species. The ranges of the two species are sympatric over much of the range of *S. bicolor* eliminating geography as helpful in determining which of the two species one has in hand. Fernald (1950) used a difference in phyllary traits as a secondary character to separate *S. bicolor* and *S. hispida*; phyllaries of *S. bicolor* purportedly had a more contrasting color difference between the green tip and the whitish to straminous bases and margins, while phyllaries of *S. hispida* had less contrasting color differences. Our examination of phyllaries of herbarium collections of the two species did not confirm this to be a reliable character, although some of the *S. bicolor* specimens had narrower zones of green pigmentation which might lead to the impression that the phyllaries of *S. bicolor* had a more obvious green to white contrast than on phyllaries of *S. hispida.* Differences in drying techniques and the age of specimens could also influence such color pattern differences. A preliminary observation that there might be a difference in degree of clavateness of the long inner pappus bristles resulted in the detailed investigation of pappus variation in the entire genus *Solidago*, but also resulted in the conclusion that *S. hispida* and *S. bicolor* had similarly moderately clavate long inner bristles (Hood & Semple 2003). In the two species a priori group analysis of *S. bicolor* and *S. hispida*, the technical traits of upper leaf width, inner phyllary length, disc floret pappus length at anthesis, and ray floret lamina length were selected to separate the two species with 81% and 84% of the specimens, respectively being assigned a posteriori to their a priori group (see Table 15) without using ray floret color.

In the *Solidago bicolor-S. roanensis-S. sciaphila* analysis, all three specimens of *S. bicolor* assigned to the other species groups a posteriori were from portions of the range of *S. bicolor* well outside the ranges of *S. roanensis* and *S. sciaphila*. All three had white rays. Clearly, these were specimens with atypical values for the traits used to separate the taxa in the STEPWISE analysis (disc floret pappus length, upper leaf length, and ray floret lamina length) and were not previously unrecognized members of species not known to be present in Ontario, Nova Scotia or Prince Edward Island.

Solidago sciaphila can be confused with *S. hispida* and *S. speciosa.* It has the most serrations on mid and upper stem leaves of any of the three species, but the leaves can be entire. The results of the three species analysis of specimens of *S. hispida*, *S. sciaphila*, and *S. speciosa* strongly support recognition of the three species with high probability of correct assignment and placement. Nonetheless, some collections from areas where the ranges of the three species are sympatric can be

difficult to assign to species. Tall plants of *S. sciaphila* from wooded slopes with loamy soil are the most likely to be confused with the generally much taller *S. speciosa*. In the analysis of the three species, the specimens of *S. hispida* assigned to *S. sciaphila* and *S. speciosa* came from parts of the range of *S. hispida* that are not sympatric with either species and had stem hair traits that would place them in *S. hispida*. The one collection of *S. speciosa* (*Semple & Chmielewski 6103* WAT, Lancaster Co., South Carolina) that was assigned in the three species analysis to *S. hispida* with 72% probability came from the edge of the Piedmont where *S. hispida* does not occur; also the specimen was 177 cm tall which is more than double the average height of *S. hispida*. In the study of the *S. speciosa* complex reported by Semple et al. (2017), *Semple & Chmielewski 6103* WAT was placed in *S. erecta* with 60% probability in the 14 species analysis, into *S. erecta* with 80% probability in the *S. speciosa-S. erecta-S. rigidiuscula* analysis, and into *S. speciosa* with 98% probability in the *S. jejunifolia-S. pallida-S. rigidiuscula-S. speciosa* analysis. The specimen is much too tall at 177 cm to be *S. erecta*. This, of course, is the challenge of working with *Solidago*. The specimen was annotated as *S. rigidiuscula* in 2012 by the first author, but the results of the analyses do not support that conclusion. Unfortunately, some individuals of *Solidago* can have atypical traits for the species they are members of and show technical affinities to species well outside their provenance or have other traits that are even more atypical for the other species. Alternative methods for assigning such specimens to a species are needed for those cases when correct identification is critical.

Solidago sciaphila is the only tetraploid in the *S. bicolor* complex. It is the only upper Midwestern USA endemic in the complex. Its range is much of the Driftless area of southeastern Minnesota, southwestern Wisconsin, and adjacent Illinois and Iowa, which was unglaciated during the last glaciation that peaked some 25,000 years ago. If not a refugial area for *S. hispida* like plants at peak glaciation, the area certainly would have been recolonized earlier than areas to the north and east and thus might have provided conditions favoring divergence into a distinct new taxon that is the only tetraploid species in the *S. bicolor* complex. It is unknown whether it is the result of autopolyploidy and subsequent loss of the diploid ancestors or the result of allopolyploidy involving two diploid parent species.

Data on character trait ranges and means for *Solidago bicolor*, *S. erecta*, *S. hispida*, *S. roanensis*, and *S. sciaphila* are summarized in Table 15. The means are based on all raw scores for each character. Only mean values were used in the analyses. The data is only for specimens included in the analyses and more extreme values for numbers and sizes of parts will likely be encountered. Ovary/fruit traits were measured on florets from flowering heads and do not represent mature fruit values. A detailed description of *S. porteri* was included in Semple & Estes (2014).

Table 15. Descriptive statistics on raw data on morphological traits of specimens used in the multivariate analysis *S. bicolor*, *S. erecta*, *S. hispida*, *S.* roanensis, and *S. sciaphila*: min-**mean**-max; * traits selected in STEPDISC analyses. Abbreviations of traits are described in Table 1.

Trait	*S. bicolor*	*S. erecta*	*S. hispida*	*S. roanensis*	*S. sciaphila*
STEMHT cm	15–**59**–104	53–**80**–116	5–**39.4**–100.5	26–**61.2**–101	19–**51.6**–77.7
BLFLN mm	22–**92.8**–180	97–**132**–164	7–**70.9**–175	9.5–**93.3**–185	30–**131.6**–290
BLFPETLN mm	6–**41.4**–101	40–**43.2**–50	2.7–**29.3**–85	4.5–**48.8**–110	16–**46**–120
BLFWD mm	7–**18.5**–35	19–**29**–40	1.5–**17.9**–52	2.3–**20.4**–36	19–**38.1**–68
BLFWTOE mm	8–**22.9**–45	15–**33**–40	1–**17.6**–55	2.3–**25.9**–80	16–36.6–65
BLFSER	0–**8.5**–29	0–**2.4**–6	0–**6.3**–23	4–**10.2**–21	2–**10.4**–19
LLFLN mm	26–**103**–159	42–**80.5**–144	7.7–**62.3**–157	10.5–**85.6**–150	42–**98.5**–175
LLFWD mm	6–**23.8**–43	7.5–**16.9**–39	1.7–**16.3**–50	2.4–**20.9**–42	14–**32.2**–55

LLFWTOE mm	10–**34.2**–62	10–**26.8**–78	2–**18.7**–50	3.4–**31.5**–55	15–**34.5**–60
LLFSER	0–**8**–17	0–**5.4**–26	0–**6.2**–28	5–**11.1**–20	2–**10.7**–19
MLFLN mm	12–**63.2**–123	22–**50.9**–87	3–**42.5**–102	7–**64.8**–125	10–**55.9**–115
MLFWD * mm	2–**15**–27	5–**10.4**–20	1.5–**11.3**–72	2–**16.3**–32	7–**19.6**–46
MLFWTOE mm	6–**27.3**–65	7–**21.7**–37	1.5–**16.6**–118	2.9–**31.2**–55	11–**25.5**–57
MLFSER*	0–**6.1**–16	0–**2.8**–14	0–**4.3**–17	1–**7.7**–20	0–**5.3**–17
ULFLN* mm	13–**40**–65	12–**28.3**–57	1.6–**28.5**–67	4–**39.9**–81	15–**33.8**–95
ULFWD* mm	3–**10.4**–19	2–**5.5**–13	0.6–**7**–18	1–**9.4**–19	3–**9.8**–32
ULFWTOE mm	6–**18.7**–35	4–**11.5**–31	0.7–**11.3**–35	2–**20.1**–41	6–**14.3**–40
ULFSER	0–**3**–13	0–**0.5**–7	0–**1.1**–8	0–**4.2**–14	0–**1.7**–10
CAPL cm	5.5–**21.4**–47	8.4–**25.8**–72	2.3–**14.6**–56	5.2–**16.4**–29.2	5.8–**14.3**–10
CAPW cm	1.5–**5.5**–20	1.5–**4**–12.8	1–**3.1**–27	1.8–**2.8**–7	1.3–**3.5**–16
INVOLHT* mm	2.6–**4.1**–6	3.2–**4.4**–6	2.5–**4.4**–6.5	2.3–**3.9**–5.6	3.1–**4.4**–6
OPHYLN* mm	0.9–**1.4**–2.1	1–**1.7**–2.5	0.75–**1.6**–3	0.5–**1.6**–2.8	1.1–**1.8**–2.8
IPHYLN* mm	1.9–**3.2**–4.5	2.4–**3.6**–4.8	1.2–**3.5**–4.8	2.1–**3.4**–4.8	2.5–**4.0**–5.2
RAYNUM*	3–**8**–15	4–**6.5**–10	3–**8.3**–16	2–**6**–13	3–**6.7**–14
RLAMLN* mm	1–**1.9**–2.7	1.4–**2.8**–4	0.5–**2.1**–3.5	1–**1.9**–3	1.5–**2.1**–3.2
RLAMWD* mm	0.15–**0.5**–1.1	0.2–**0.76**–1.9	0.1–**0.68**–1.5	0.4–**0.73**–1.6	0.3–**0.7**–1.2
RACHLN* mm	0.6–**1.4**–2.5	0.85–**1.6**–3.3	0.3–**1.3**–2.4	0.5–**1.2**–2.1	0.7–**1.6**–2.7
RPAPLN mm	1.8–**2.9**–3.8	1.9–**3.4**–5	1.1–**2.7**–4.2	1.3–**2.3**–3.1	1.3–**2.3**–3.3
DISCNUM	5–**10.5**–16	4–**9.5**–15	3–**10**–24	4–**8.6**–13	1–**8.7**–15
DCORLN mm	3–**3.9**–5.1	1.8–**4.4**–7.4	2.2–**4.2**–5	2.5–**3.6**–4.9	2.3–**3.7**–6.5
DLOBLN mm	0.3–**0.81**–1.5	0.25–**0.7**–1	0.2–**0.9**–1.5	0.2–**0.8**–1.7	0.2–**0.84**–1.2
DACHLN mm	0.7–**1.4**–2.5	0.9–**1.6**–3.1	0.5–**1.3**–2.5	0.6–**1.2**–2.3	0.8–**1.5**–2.6
DPAPLN* mm	1.9–**3.3**–4.4	2.5–**4**–5	1.2–**3.3**–5	1.5–**2.8**–4.2	2–**3**–4.3

Analyses of varieties of *Solidago hispida*

Fernald (1908, 1915) proposed four varieties in *Solidago hispida* – var. *arnoglossa*, var. *disjuncta*, var. *lanata*, and var. *tonsa* – which he stated were "well marked". The holotypes of var. *arnoglossa*, var. *disjuncta*, and var. *tonsa* are all from within about 30 km of Corner Brook, Newfoundland in different habitats. The type of var. *disjuncta* (*Fernald, Wiegand & Kittredge 4071*; holotype: GH!; isotypes: NY!, US on line image!) is a small plant with a densely woolly stem and may be nothing more than a dwarf individual of the "var. *lanata*" extreme indument morph or var. *hispida*; no densely woolly-stemmed plants from Newfoundland were included in the sample of var. *hispida* in this study. The type of var. *arnoglossa* is (*Waghorne s.n.*, holotype: GH!) includes two shoots about 34 cm tall, lower stems that are moderately hispidulo-strigose, and a basal rosette with the largest leaf about 12 × 5 cm with crenulo-serrate margins. The type of var. *tonsa* (*Fernald & Wiegand 4075*, holotype: GH!) includes five shoots 19-49 cm tall, stems that are very sparsely to sparsely woolly, and lower stem leaves that vary noticeably between shoots in margin serration size but are generally oblanceolate and acute. The smaller lowest leaves are subspathulate, obovate, and obtuse to rounded, which is a common in many species of *Solidago*.

The two analyses of the varieties of *Solidago hispida* indicate that there are differences among var. *arnoglossa*, var. *hispida*, var. *huronensis*, and var. *tonsa* but that the varieties are not strongly separated and intermediates occur. Further research is needed to fully assess the usefulness

of recognizing these varieties. In the analysis without stem height included as a trait, outer phyllary length, numbers of ray florets, and disc floret pappus length were selected as discriminating traits, but only 50% of the specimens of var. *arnoglossa* were placed a posteriori into var. *arnoglossa*. In the second analysis with stem height included, stem height along with outer phyllary length, numbers of ray florets and disc floret pappus length were selected to separate taxa; 75% of the specimens of var. *arnoglossa* were placed a posteriori into var. *arnoglossa*. Thus, stem height is critical in separating var. *arnoglossa* from var. *tonsa*. The same was true in the case of var. *hispida* for which 76% of specimens in the first analysis were assigned a posteriori to var. *hispida*, but 85% in the second analysis with stem height included. However, the shortest specimen of var. *hispida* (*Semple & Brammall 2864* WAT; 13.8 cm tall stem shoot growing on Gneiss shoreline rocks of Lake Superior, Algoma Dist., Ontario) was assigned a posteriori to var. *hispida* with 53% probability in the first analysis (24% to var. *huronensis*), but in the second analysis when stem height was included as a trait the specimen was assigned a posteriori to var. *arnoglossa* with 82% probability (10% to var. *hispida*). Inclusion of stem height had little effect overall with placement in var. *huronensis* dropping from 73% a posteriori placement to var. *huronensis* in the first analysis to 70% in the second analysis. As noted above, stem height is a highly plastic trait in *Solidago* greatly influenced by growing conditions from one season to the next and by soil richness and moisture content. Stem height did not correlate strongly with other characters in any of the analyses done on members of subsect. *Squarrosae*, although generally smaller plants had small leaves. Var. *tonsa* is from habitats that likely result in stunted growth. Transplant studies would be useful in determining whether stem height is genetically limited or just a consequence of habitat growing conditions in this case. The var. *tonsa* appears to be a genetically based ecotype, but this needs confirmation.

The more northern shorter collection from Newfoundland included in the var. *hispida* a priori group (*Morton & Venn NA12163* TRT) was placed a posteriori into var. *tonsa* in both analyses with high probability (91% and 93%). The southern two taller shoots from Newfoundland included in the var. *hispida* a priori group (*Morton & Venn NA12438* TRT) were placed a posteriori into var. *hispida* in both analyses with high probability (87% and 75% in the analysis without stem height and 94% and 90% in the analysis with stem height included). Thus in these latter two cases stem height was not critical in the a posteriori placement of the var. *hispida* specimens from Newfoundland; the short plant went to var. *tonsa* even when stem height was not included. Stem hair density was similar and moderately dense in both of the collections and mid-range for var. *hispida* but high for var. *tonsa*. A larger sample size of var. *hispida* plants from Newfoundland is needed to further explore differences between var. *hispida* and var. *tonsa* in Newfoundland.

Results are ambivalent about the identity of the four specimens treated as var. *arnoglossa* from central and eastern Québec (3 shoots, *Morton & Venn* NA15322 TRT from Mistassini, Québec; 1 shoot *Morton* NA3978 TRT from Bic Island, Gaspé, Québec; red dots on map in Fig. 11). In the first analysis without stem height included, these specimens were assigned a posteriori in the analysis to var. *arnoglossa* with 71% probability (shoot #2, *Morton & Venn* NA15322 TRT) and to var. *hispida* with 84% (*Morton* NA3978 TRT), 64% and 60% (shoot #1 and shoot #3, *Morton & Venn* NA15322 TRT). In the analysis with stem height included as a discriminating trait, the four specimens were assigned a posteriori to var. *arnoglossa* with 96% (shoot #2, *Morton & Venn* NA15322 TRT; 23 cm tall), 82% (shoot #3, *Morton & Venn* NA15322 TRT; 19 cm tall) and 56% (shoot #1, *Morton & Venn* NA15322 TRT; 15 cm tall) and to var. *hispida* with 71% probability (*Morton* NA3978 TRT; 40 cm tall). Stem height was significant in placing the specimens to variety. The Bic Island collection was very sparsely hairy on the leaves and stems, while the Mistassini collections were moderately villous on the stem and strigose on the basal leaves. The short Mistassini plants are more likely just short members of var. *hispida*. The Bic Is., Gaspé plant is likely a less hairy member of var. *hispida*. A larger sample size of *S. hispida* from the eastern Gaspé and from all of Newfoundland is need to explore how distinct var. *arnoglossa* is from var. *hispida*.

As treated here, var. *hispida* includes plants with a wide range of variation in stem pubescence ranging from densely long-woolly ("var. *lanata*") to sparsely hispid-woolly (Figs. 4 A-D). Also included was a plant with canescent stems that had short strigose hairs (*Baldwin 11518* WAT from Saskatchewan; Fig. 4E). If the densely long-woolly morph is recognized as a separate variety, then the short-canescent morph should also possibly be recognized as a distinct variety. Our observations on stems indicated that the densely-woolly morph is just an extreme in a continuum of hair density and length. We did not include sufficient numbers of variously canescent stemmed plants in this study to reach a similar conclusion. A detailed study of stem hair density and length would be a useful analysis to clarify the range of variation on short-haired stems in *Solidago hispida* including more samples from Saskatchewan and Newfoundland. *Solidago hispida* is the only species in the *S. bicolor-S. hispida* complex with multiple varieties. A DNA based analysis of the distribution of distinct haplotypes and how these correlate with proposed varieties would also be useful, if sufficient variation in DNA sequence data occurs in the species.

Descriptive statistics on raw data on morphological traits of specimens used in the multivariate analysis the varieties of *Solidago hispida* are presented in Table 16. Values in the table are only from the specimens included in the multivariate analyses. More extreme values for minimum and maximum for each trait for each species are likely to be encountered. Ovary/fruit values were taken from florets of heads in bloom. Mature fruits are bigger with longer pappus bristles.

Table 16. Descriptive statistics on raw data on morphological traits of specimens used in the multivariate analysis the varieites of *S. hispida*: min-**mean**-max. No data for basal leaves of *S. rigidiuscula* at flowering. The lowest stem leaves are also generally absent by flowering. * traits selected in STEPDISC analyses.

Trait	var. *arnoglossa*	var. *hispida*	var. *huronensis*	var. *tonsa*
STEMHT* cm	5–**20.5**–40.4	11.5–**50**–100.5	26–**43**–66	7–**16.1**–30.7
BLFLN mm	30–**70**–135	7–**79.8**–175	30–**70**–145	21–**40.8**–79
BLFPETLN mm	12–**31.8**–75	2.7–**31.6**–80	8–**31.4**–85	7–**20.1**–79
BLFWD mm	7–**17.7**–36	1.5–**19.9**–50	10–**19**–31	5–**10.6**–17
BLFWTOE mm	5–**15.2**–40	1–**21.5**–55	10–**19.7**–7.5	4–**8.6**–17
BLFSER	0–**5.7**–12	0–**7.6**–28	3–**6.4**–15	3–**5.3**–10
LLFLN mm	10–**49.9**–95	7.7–**67**–157	27–**66.9**–137	19–**47.7**–70
LLFWD mm	5–**11.6**–25	1.7–**17.9**–50	8–**18.3**–37	6–**11.7**–18
LLFWTOE mm	3–**11**–27	2–**21.5**–50	8–**21.8**–37	5–**10.1**–16
LLFSER	0–**4**–10	0–**7.6**–28	2–**9.3**–25	2–**6**–9
MLFLN mm	20–**41.9**–80	4–**45**–92	14–**34.1**–102	19–**43.4**–69
MLFWD mm	3–**10.7**–21	1.5–**12.2**–72	3–**9.5**–30	3–**9.3**–17
MLFWTOE mm	5–**10.9**–20	1.5–**19.3**–50	6–**14.8**–32	5–**11.1**–20
MLFSER	0–**3**–9	0–**4.4**–17	0–**4**–16	0–**5.5**–9
ULFLN mm	16–**32.8**–57	1.6–**29.5**–67	7–**19.1**–58	11–**31.3**–61
ULFWD mm	3–**8.1**–15	0.6–**7.2**–16	2–**5**–18	2–**6.5**–12
ULFWTOE mm	4–**9.8**–19	1–**12.6**–35	2–**9**–23	3–**9.2**–20
ULFSER	0–**1.2**–6	0–**0.9**–8	0–**1.3**–5	0–**1.9**–6
CAPL cm	2.5–**10.5**–22	4.5–**18.2**–56.5	5–**12.4**–27.3	2.3–**7.5**–17
CAPW cm	1.6–**2.5**–4.7	1–**3.1**–8.1	1.4–**4.9**–27	1.2–**1.9**–3.6
INVOLHT mm	3.2–**4.5**–5.3	2.5–**4.3**–6.5	3–**4.5**–5.9	2.5–**4.6**–6.5
OPHYLN* mm	0.75–**1.8**–2.5	0.85–**1.3**–2.1	0.9–**1.6**–2.2	0.9–**1.9**–3

IPHYLN mm	2.5–**3.8**–4.7	2.3.–**3.5**–4.8	1.2–**3.5**–4.8	2.1–**3.2**–3.9
RAYNUM*	4–**9.8**–16	3–**8**–14	3–**8**–14	5–**9.1**–14
RLAMLN mm	1.5–**2.4**–3.3	1.5–**2.1**–3.5	1–**2.1**–3.5	1.2–**2.0**–2.8
RLAMWD mm	0.5–**0.75**–1.1	0.1–**0.68**–2	0.1–**0.7**–2	0.3–**0.6**–1
RACHLN mm	0.65–**1.3**–2	0.5–**1.3**–2	0.5–**1.3**–2	0.8–**1.3**–2
RPAPLN	2.1–**2.9**–3.7	1.3–**2.7**–4.2	1.3–**2.7**–4.2	1.9–**2.4**–3.3
DISCNUM	4–**11.1**–18	3–**9**–24	3–**9.4**–24	8–**11.8**–16
DCORLN	3.5–**4.3**–5.2	2.2–**4.2**–5	2.2–**4.1**–5	2.7–**3.9**–5
DLOBLN	0.5–**0.77**–1	0.2–**0.9**–1.1	0.2–**0.94**–1.3	0.5–**0.9**–1.5
DACHLN	0.85–**1.3**–2	0.5–**1.3**–2.5	0.5–**1.3**–2.5	0.7–**1.3**–2
DPAPLN*	2.1–**3.4**–4.25	2.1–**3.3**–6	2.1–**3.3**–5	2.3–**2.9**–3.7

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UPDATE ON THE DISTRIBUTION
OF THE NARROWLY ENDEMIC *PAYSONIA LESCURII* (BRASSICACEAE)

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ABSTRACT

Paysonia lescurii (A.Gray) O'Kane & Al-Shehbaz [formerly *Lesquerella lescurii* (A.Gray) Watson], Nashville or Lescur's Bladderpod, is apparently endemic to 10 contiguous counties in central Tennessee, one county in south-central Kentucky, and ostensibly from one county in northern Alabama. Recent field, herbarium, and literature studies indicate that the species is extant and often abundant at numerous sites in the 10 Tennessee counties. One Kentucky location is well documented but the species has not been seen there since 1985. Documentation is apparently lacking for the Alabama reports and the species, at this time, should not be considered part of the flora of that state.

The genus *Lesquerella* was established by Watson (1888), commemorating paleontologist and bryologist Leo Lesquereux (1806-1889); 33 species were recognized. Payson (1921) monographed the genus, raising the number of species to 52. Rollins (1993), who studied the genus extensively, recognized 83 species in North America, noting that the distribution is centered in the southwestern United States and Mexico with one species distributed across the Canadian Artic from Greenland into Alaska and Siberia. At least five additional North American species have been described and several taxa occur in South America (Al-Shehbaz & O'Kane 2002).

Five species of the former genus *Lesquerella* are known to be present in Tennessee (*L. densipila, globosa, lescurii, perforata, stonensis*); two of these occur in Kentucky (*L. globosa* and *lescurii*) and one in Alabama (*L. densipila*, plus the Alabama endemic *L. lyrata*) (Atlas of Tennessee Vascular Plants 2017; Cranfill et al. 1985; Keener et al. 2017; Kral et al. 2011; Rollins 1952, 1955, 1993; Rollins & Shaw 1973; Tennessee Flora Committee 2015). Recently, one of these six taxa (*L. globosa*) was transferred to the existing genus *Physaria* (Al-Shehbaz & O'Kane 2002) and the other five to the newly-erected genus *Paysonia*, commemorating monographer E.B. Payson (1893-1927) (O'Kane & Al-Shehbaz 2002). In addition to these six species, *Physaria gracilis* (Hook.) O'Kane & Al-Shehbaz subsp. *gracilis* [*Lesquerella gracilis* (Hook.) Watson], mostly a midwestern species, was reported as possibly adventive in Alabama and Tennessee by O'Kane (2010), but it is not included in recent accounts of the flora of either state (Kral et al. 2011; Keener et al. 2017; Tennessee Flora Committee 2015). Additional study of this species in Alabama and Tennessee is warranted.

The purpose of this report is to update distribution data and provide some additional information on one of the former *Lesquerella* species, the narrowly endemic *Paysonia lescurii* (A.Gray) O'Kane & Al-Shehbaz, commonly referred to as Nashville or Lescur's Bladderpod.

Paysonia lescurii is a small (usually <1.5 dm, rarely >2.5 dm in height), flowering from late February to early May (Figs. 1, 2, photographs by the author). Distinctive, flattened fruits [siliques sensu Rollins (1993), silicles sensu O'Kane (2010) (Fig. 3)] mature and seeds are shed April–early June. Baskin et al. (1992) showed that seeds are dormant at maturity and require high summer temperatures to break dormancy. The species is a typical winter annual with germination occurring in autumn and flowering/fruiting the following spring. However, some seeds remain dormant (enter secondary dormancy) and a persistent seed bank is formed.

Habitats include hillsides, cedar glades, riverine flood plains, old fields, roadsides, vacant lots, and pastures. Early spring stands often cover several hectares before tillage in bottomland fields of the Cumberland River that were tilled the previous year (Figure 1). These large spring displays verify the comment by Rollins (1981) that the species has weedy tendencies.

Listed Status

Federally, *Paysonia lescurii* (as *Lesquerella*) was considered threatened by Ayensu and DeFillips (1978) but later removed from consideration as a federal candidate (U.S. Fish and Wildlife Service 1985) because it was found to be "more abundant and widespread than previously believed and not subject to the degree of threats to warrant status." In Tennessee, the species was listed as threatened by Collins et al. (1978) but later delisted (Somers 1989) for the reasons noted above. The species is very rare in Kentucky (Cranfill et al. 1985) and listed there as Historic (Kentucky State Nature Preserves Commission 2012).

Distribution

Tennessee: Extant populations are known from 10 Tennessee counties (Atlas of Tennessee Vascular Plants 2017), i.e., Cheatham, Davidson, Dickson, Montgomery, Rutherford, Smith, Sumner, Williamson, Wilson, and Stewart (Figure 4). The distribution is centered in the Central (Nashville) Basin, Davidson and surrounding counties. The Cumberland River, which flows northwestwardly through the Basin, has apparently provided a migratory pathway to the Western Highland Rim counties of Cheatham, Dickson, Montgomery, and Stewart in Tennessee, and Trigg County in Kentucky (Fig. 4). In these counties the species is almost exclusively found in Cumberland River bottomlands (Fig. 1), which are occasionally flooded by river overflow or backwaters.

Kentucky: The only report from the state was by Chester (1982) from Trigg County (Figure 4). The bottomland site is on the west side of the Cumberland River within Land Between The Lakes, a U.S. Forest Service National Recreation Area. Prior to 1983, this small bottomland site was planted yearly in corn or other crops for wildlife food. Thereafter, the site was seeded to perennial grasses and is in a successional stage today. Fitch et al. (2007) showed that populations of several species of *Paysonia* are enhanced by agricultural disturbance and do not compete with perennial grasses. The species has not been seen in Kentucky since 1985 (Campbell & Medley 2012; Kentucky State Nature Preserves Commission 2012). Impoundment of the Cumberland River by Barkley Dam in 1966 destroyed much of the suitable habitat for the species in Kentucky. Continued searches of remnant bottomlands north of the Tennessee border have been unfruitful to date.

Alabama: Kral (1983) first reported the species from the state (Limestone County, Fig. 4). Rollins (1993), in his comprehensive treatment of the Brassicaceae for North and Central America, reported the species from northern Alabama without citation but referenced Kral (1983) in the literature cited. Al-Shehbaz (1987) noted presence of the species in Alabama, specifically crediting Kral (1983). Others including Alabama in the distribution are O'Kane (2010), USDA, NRCS (2017) and Weakley (2015).

I have not been able to verify the Alabama reports. There are no specimens from Alabama at the Gray Herbarium (GH), where the majority of *Lesquerella* collections by Dr. Rollins are housed (e-mail from Anthony Brach, Curatorial Assistant, Harvard University Herbaria, to Dr. Brian Keener, 24 February 2016). A comprehensive study of the Limestone County flora (Hofmann 1999) found only *Lesquerella densipila* Rollins. The species is not included for the state by Kral et al. (2011), Keener et al. (2017), or Kartesz (2015).

The original Alabama report (Kral 1983) was apparently based on a specimen collected 29 Mar 1958, *J.P. & M. Gillespie 893*. The herbarium label indicates Florida State University but the specimen now is at BRIT (image supplied by Tiana Rehman, BRIT Collections Manager, 1 February

2017).   The sheet contains 16 entire or partial plants in flower-bud stage, originally identified as *Barbarea verna*.   Dr. Kral annotated the specimen in 1968 as *Lesquerella lescurii* (Gray) Watson (written on sheet directly above the original label).   In 1986, Dr. Rollins attached an annotation label in the upper left, noting: "Lesquerella, more likely L. densipila Rollins – Too young to be sure." (quotation marks are those of this author).   Location information on the label indicates "Roadside 3 miles north of Owens Junior High School on highway #60."   Interestingly, current Highway 60 is a short section on uplands south of the school (now Owens Elementary School).   Three miles north of the school place the collection site within the floodplain of the Elk River, a suitable habitat for both *P. densipila* and *P. lescurii*.

Roadsides along current Highway 60 and several Elk River agricultural floodplains were searched on 3 March 2017 by the author and Dr. David Webb; in addition, Dr. Webb searched the area again on 20 March; both searches failed to find *Paysonia*.   However, there are documented collections of *P. densipila* from the area as noted generally by Rollins (1993) and specifically by Hofmann (1999) and Keener et al. (2017).   Documentation that *P. lescurii* occurs (or ever occurred) in Alabama is apparently lacking or at least questionable.

In summary, the endemic winter annual *Paysonia lescurii* is known from 10 counties in Middle Tennessee, where it has weedy tendencies, often forming extensive early spring stands.   The species is well-documented in literature and with specimens from one site in Kentucky, but it exists there now as a seed bank if at all.   Reports from Alabama apparently have been based on an immature *Lesquerella* (*Paysonia*) specimen of questionable identity and the species should not be considered part of the Alabama flora unless indicated by new data.   The life cycle is not unlike that of many widespread winter annuals and the question posed by Payson (1921) has yet to be answered: "One wonders what the limiting factors in it distribution may be."

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Figure 1. *Paysonia lescurii* in a bottomland field, Cheatham County, Tennessee. The Cumberland River is just past tree line on left. Field was cultivated in soybeans in 2016. Image taken 24 February 2017

Figure 2. Flowers of *Paysonia lescurii*; petals 5-7 mm long. Same site as Figure 1. Image taken 10 March 2017.

Figure 3. Distinctive, flattened fruits of *Paysonia lescurii*, each fruit 4-6 mm long, 3-4 mm wide. Same site as Figure 1. Image taken 22 April 2017.
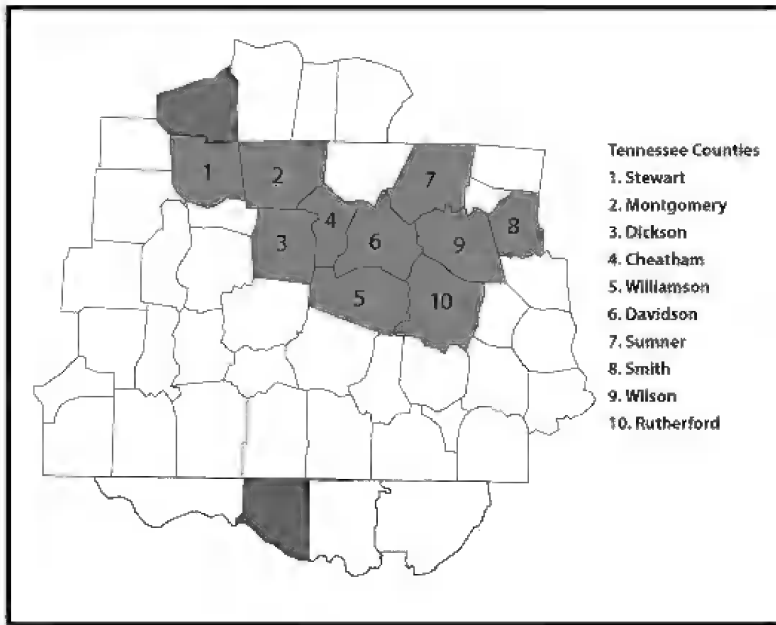
Figure 4. Known and reported county distribution of *Paysonia lescurii*. Blue = Trigg County, Kentucky (Historic, documented from one site); Orange = ten counties in Tennessee (documented from numerous sites); Red = Limestone County, Alabama (reported but not confirmed).

LISTA ANOTADA DE LA FLORA VASCULAR
DE LA SIERRA DE MAZATÁN (HUÉRFANA),
CENTRO DE SONORA, MÉXICO

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RESUMEN

Durante un período de diez años (2005-2015), se llevó a cabo la recolecta de ejemplares de herbario y el registro de observaciones de campo en la Sierra de Mazatán (Huérfana), en una región entre Pueblo de Álamos y Rancho Viejo, municipio de Ures, Mazatán, municipio de Mazatán, y Nácori Grande, municipio de Villa Pesqueira, Sonora, México. Esta región abarca 804 kilómetros cuadrados, y se delimita por un círculo con un radio de 16 kilómetros cuyo centro se localiza en Rancho El Bachán, en las coordenadas 29.1° N y 110.191° O (Figura 1). En esta área, la vegetación corresponde principalmente al matorral desértico sonorense, matorral espinoso de pié de monte y encinal. Actualmente, la flora vascular de la Sierra de Mazatán contabiliza 626 plantas distribuidas en 384 géneros y 104 familias. Las familias con mayor número de especies son Asteraceae (77), Fabaceae (72), Poaceae (62), Euphorbiaceae (29), Malvaceae (25), Cactaceae (20), Convolvulaceae (19), Solanaceae (17), Acanthaceae (16) y Plantaginaceae (14), incluyendo 17 especies de helechos y plantas afines. En la zona estudiada, se han descubierto cuatro especies nuevas de plantas; además, la especie en peligro de extinción, *Dioon sonorense*, alcanza aquí su límite de distribución norte.

ABSTRACT

Herbarium specimens were collected and plants observed in the field in the Sierra de Mazatán (Huérfana) between Pueblo de Álamos and Rancho Viejo, Ures Municipality, Mazatán, Mazatán Municipality, and Nácori Grande, Villa Pesqueira Municipality, in Sonora, Mexico, from 2005-2015. This region covers 804 square kilometers in a circle with a radius of 16 kilometers, the center located in Rancho El Bachán (Fig. 1). In this area, the vegetation corresponds mainly to Sonoran desertscrub, foothills thornscrub, and oak woodland. Currently, the vascular flora of the Sierra de Mazatán includes 626 species distributed in 384 genera and 104 families. The families with the highest number of species are Asteraceae (77), Fabaceae (71), Poaceae (65), Euphorbiaceae (27), Malvaceae (25), Cactaceae (21), Convolvulaceae (18), Solanaceae (17), Acanthaceae (16), and Plantaginaceae (14), including 17 species of ferns and related plants. In the study area, four new species of plants have been discovered; in addition, the endangered species *Dioon sonorense* reaches its northernmost range.

La Sierra de Mazatán se localiza en la región central de Sonora, en los municipios de Mazatán y Ures, a lo largo de la carretera estatal 104 Hermosillo-Sahuaripa (Fig. 1), alcanzando los 1545 metros de altitud en el cerro El Sainito. Según la Comisión para el Uso y Conocimiento de la Biodiversidad (CONABIO), la Sierra de Mazatán es una *isla* de biodiversidad templada rodeada por un paisaje árido del desierto de Sonora (Arriaga 2000). La Sierra de Mazatán pertenece a la región fisiográfica de la Llanura Costera del Noroeste y la subprovincia Sierra Madre Occidental (Rzedowski 1981).

Figura 1. Localización de la Sierra de Mazatán y área de la flora. Mapa elaborado por Carlos Alberto Enciso-Miranda.

Por su geología, la Sierra de Mazatán puede considerarse como un sitio excepcional y único en su género en México. Es un núcleo metamórfico originario del período terciario (Comisión Nacional de Áreas Naturales Protegidas, 2012). La composición de la roca incluye principalmente rocas metamórficas, aunque el Cerro Prieto, situado en el borde suroeste de la sierra, está conformado de piedra caliza (Navarro, 1985). Además, en el área de los poblados de Nácori Grande y Mazatán hay piedras sedimentarias, al igual que en las faldas de la sierra. Otros cuatro núcleos metamórficos existen en Sonora pero, sin lugar a dudas, la Sierra de Mazatán representa el ejemplo más característico. Además, en su ladera poniente, existe un gran afloramiento de un granito orbicular, el segundo afloramiento de una roca de este tipo en México después de la Sierra San Pedro Mártir, en Baja California. Pocos ejemplos de rocas de este tipo existen en el mundo y el granito orbicular por si solo justificaría el establecimiento de una área natural protegida (Comisión Nacional de Áreas Naturales Protegidas, 2012).

El clima es cálido hacia la parte sureste, con una temperatura media anual de 23.8°C; mientras que en la parte alta de la sierra, el clima es más suave con inviernos fríos con la temperatura más baja de 18°C (Morales-Abril y Parra-Salazar 1994). La Sierra de Mazatán funciona como un corredor biológico, ya que permite las interacciones entre la biota del Desierto Sonorense y de la Sierra Madre Occidental (Arriaga, 2000).

Las islas serranas o islas del cielo (en inglés, sky islands), también llamado Archipiélago Madrense, son un punto crítico de biodiversidad en el noroeste de México y el suroeste de los Estados Unidos. Esta ecoregión lleva su nombre gracias a las 55 sierras de encinal o pino-encino, o "islas", que comprende, cada una rodeada de un "mar" de pastizal, matorral espinoso o matorral desértico. Estas islas serranas aisladas van desde por debajo de los 500 a más de 3300 metros de altitud, conectan la meseta del Colorado y el norte templado con la Sierra Madre Occidental y los trópicos del Nuevo Mundo (Van Devender et al. 2013). En la actualidad, la Sierra de Mazatán es la isla serrana más al sudoeste en Sonora, a sólo 70 km al este de Hermosillo, la capital del estado. Oficialmente, se le denomina Sierra de Mazatán (INEGI 1995), y así se refieren a ella los pobladores del municipio de Mazatán; sin embargo, la mayor parte de la montaña pertenece a las Comunidades Agrarias de Pueblo de Álamos y Rancho Viejo en el municipio de Ures, donde es reconocida como Sierra Huérfana ó Sierra Cuadrada. El nombre Mazatán proviene de una palabra indígena náhuatl que significa "lugar de venado". Está rodeada de colinas tropicales justo al este del Desierto Sonorense, con bosques de encinos en la parte superior con un paisaje formado por cantos rodados de granito blanquecino (Van Devender 2014).

La ganadería es la actividad productiva tradicional y predominante en la Sierra de Mazatán, y la producción de queso a pequeña escala es una actividad económica suplementaria muy importante para los ganaderos. En el pasado, la minería a pequeña escala fue una actividad económica importante en la sierra; ahora, todas estas minas están abandonadas y no se conocen planes para reabrirlas a corto plazo (Sánchez-E. 2004). Actualmente, el turismo en la zona es una actividad ocasional creciendo en importancia, especialmente durante las épocas de vacaciones cuando la región atrae a algunos visitantes, sobre todo para ocupar las cabañas que se han establecido en el encinal de la parte alta de la Sierra.

La Sierra de Mazatán corresponde probablemente a la región más preservada en un radio de 100 kilómetros alrededor de la capital del estado, Hermosillo (Comisión Nacional de Áreas Naturales Protegidas 2012), por lo que es muy importante tener un amplio conocimiento de su diversidad biológica.

ANTECEDENTES

En mayo de 1957, Howard S. Gentry recolectó una cícada en la Sierra Huérfana; 40 años más tarde, fue descrita como *Dioon sonorense*, una especie endémica de Sonora y del norte de Sinaloa. La palma de la vírgen, nombre común con el cual es conocida, ocurre en 5-6 poblaciones en Sonora, y tiene categoría de en peligro de extinción bajo la Norma Oficial Mexicana para especies con categoría de riesgo (Diario Oficial de la Federación 2010). Hay 14 especies de *Dioon* desde Nicaragua hasta el noroeste de México y la especie de la Sierra Huérfana viene a ser la cícada más septentrional del mundo (Van Devender 2014).

En 1992, la Sierra de Mazatán fue incluida en el Sistema de Áreas Naturales Protegidas del Estado de Sonora (Garza Salazar 1993). Fue propuesta como una Zona Sujeta a Conservación Ecológica Sierra de Mazatán (Morales-Abril y Parra-Salazar 1994) pero nunca fue decretada oficialmente como una reserva por el gobierno estatal. El 27 de noviembre de 2012 aparece, en el Diario Oficial de la Federación, el aviso sobre la disponibilidad pública del estudio previo justificativo para decretar la Sierra de Mazatán (Sierra Huérfana) como un Área de Protección de

Flora y Fauna; sin embargo, a la fecha de esta publicación, el gobierno mexicano no ha emitido una resolución. Por otra parte, la Comisión para el Uso y Conocimiento de la Biodiversidad (CONABIO), categorizó a la Sierra de Mazatán como una Región Terrestre Prioritaria para la conservación (Arriaga 2000).

El primer estudio sobre la flora y vegetación para la Sierra de Mazatán se llevó a cabo alrededor de 1984, registrando 137 plantas (Navarro, 1985); sin embargo, los especímenes recolectados en este trabajo no pudieron consultarse debido a que no fueron localizados en el herbario COTECOCA de Hermosillo, Sonora (Celia Bujdud, Com. Pers.).

En un inventario preliminar, realizado de 2003 a 2004, se obtuvo un listado florístico de 357 especies de plantas (Sánchez-E. 2004). Recolectas adicionales fueron llevadas a cabo del 2005 en adelante, destacando las expediciones Madrean Archipelago Biodiversity Assessment (MABA) de la organización estadounidense Sky Island Alliance, realizadas en 2014, con la participación de diversos especialistas de flora y fauna del noroeste de México y del suroeste de Estados Unidos, contribuyendo significativamente a obtener un mayor conocimiento de la diversidad biológica de la Sierra de Mazatán.

MATERIALES Y MÉTODOS

Este listado comprende la región entre Pueblo de Álamos y Rancho Viejo, municipio de Ures, Mazatán, municipio de Mazatán, y Nácori Grande, municipio de Villa Pesqueira, en el centro de Sonora, México. El área de la flora comprende 804 kilómetros cuadrados, y está delimitada por un círculo con un radio de 16 kilómetros cuyo centro se localiza en el Rancho El Bachán, en las coordenadas 29.1° N y 110.191° O (Fig. 1). Durante un período de diez años (2005 -2015), se llevó a cabo la recolecta de ejemplares de herbario y el registro de observaciones de campo. Por su cercanía a la Sierra, también se incluyeron registros de ejemplares y observaciones de campo de algunas localidades en el municipio de Villa Pesqueira, principalmente entre Nácori Grande y pueblo de Álamos.

Para elaborar el listado florístico se utilizó la herramienta para el manejo de listados florísticos (Figura 2) del portal de la Red de herbarios del Noroeste de México (Red de Herbarios del Noroeste de México 2016), clasificando los nombres de acuerdo al Diccionario Taxonómico Central de dicho portal (Symbiota Taxonomic Schema, 2016) así como el listado de la flora de Sonora (Van Devender 2010).

Este listado florístico está basado, casi en su totalidad, en las colecciones y observaciones de campo de los autores, y cada taxón en la lista está respaldado con al menos un ejemplar de herbario o una observación de campo. Los ejemplares botánicos recolectados durante el trabajo de campo fueron depositados primeramente en el Herbario de la Universidad de Sonora (USON) en Hermosillo. Un conjunto de varios duplicados se depositó en el Herbario de la Universidad de Arizona (ARIZ) en Tucson, Arizona.

Las especies con categoría de riesgo se obtuvieron de la Norma Oficial Mexicana NOM-059-SEMARNAT-2010 (Diario Oficial de la Federación 2010). La relación de plantas no nativas e invasoras se obtuvo revisando el listado de plantas no nativas e invasoras para el estado de Sonora (Van Devender 2009).

Figura 2. Listado florístico de la Sierra de Mazatán en el portal de la Red de Herbarios del Noroeste de México.

RESULTADOS Y DISCUSIÓN

La vegetación y flora de la Sierra de Mazatán resultan ser muy interesantes ya que, tras pocos kilómetros de recorrido, las comunidades vegetales cambian desde el matorral desértico sonorense de la llanura hasta matorral espinoso en la falda y el encinal en la meseta superior, esto ocurre en un gradiente altitudinal que va desde los 450 metros en la planicie desértica, hasta los 1100 y 1200 metros en las laderas norte y sur respectivamente, en la zona donde comienza el encinal (Sánchez-E. 2008).

Vegetación

Hemos considerado como las principales comunidades vegetales de la sierra de Mazatán al matorral desértico sonorense, matorral espinoso de pié de monte, bosque de encino y la vegetación de galería (Sánchez-E. 2008), aunque mas adelante se mencionan áreas de pastizal inducido en algunos claros del encinal y los mezquitales de los arroyos en las llanuras adyacentes a la sierra.

El matorral desértico sonorense se encuentra presente por debajo de los 500 metros y está representado por especies típicas de la subdivisión Planicies de Sonora; en primera instancia, por la tríada de árboles leguminosos del desierto sonorense, conformada principalmente por palo fierro (*Olneya tesota*), palo verde (*Parkinsonia microphylla*) y mezquite (*Prosopis velutina*; Sánchez-E., 2008). Otras especies arborescentes ampliamente distribuidas incluyen grandes cactos columnares como sahuaro (*Carnegiea gigantea*) y pitayo (*Stenocereus thurberi*), así como algunos arbustos o árboles bajos como ocotillo (*Fouquieria splendens*), vinorama (*Acacia constricta*), palo colorado (*Colubrina viridis*) y hierba de la flecha (*Sebastiania bilocularis*).

El matorral espinoso se encuentra desde las llanuras más bajas hasta las laderas de la sierra, en el lado oeste del área de Rancho Viejo y entre 600 y 1100 metros de altitud, la vegetación está dominada por especies de árboles y arbustos como chírahui (*Acacia cochliacantha*), torote blanco (*Bursera fagaroides* var. *elongata*), torote prieto (*B. laxiflora*), pochote (*Ceiba acuminata*), jediondilla (*Croton flavescens*), chilicote (*Erythrina flabelliformis*), palo blanco (*Ipomoea arborescens*), sanjuanico (*Jacquinia macrocarpa* subsp. *pungens*), torota (*Jatropha cordata*), mauto (*Lysiloma divaricatum*), guayabilla (*Acacia russelliana*), étcho (*Pachycereus pecten-aboriginum*), pitayo (*Stenocereus thurberi*), y uvalama (*Vitex mollis*).

Entre 1100 y 1200 metros comienza la transición hacia el bosque de encino, con una combinación de árboles y arbustos bajos como guajillo (*Acacia angustissima*), tepeguaje (*Lysiloma watsonii*), encino (*Quercus chihuahuensis*) y gloria (*Tecoma stans*). A 1300 metros, en los barrancos de esta zona de transición, encontramos pequeñas poblaciones de palma de la virgen (*Dioon sonorense*) asociadas a pochote (*Ceiba acuminata*), sotol (*Dasylirion wheeleri*, encino roble (*Quercus tuberculata*), y gloria (*Tecoma stans*). Las localidades en el lado norte de la sierra ha sido poco exploradas, aunque se han recolectado algunas especies interesantes como corcho (*Diphysa suberosa*), jícama (*Ipomoea bracteata*) y mata la sed (*Zanthoxylum fagara*) en elevaciones que van desde el pié de monte hasta los 850 metros de altitud.

En el lado oeste, a 1200 metros, el bosque de encino comienza con encino (*Quercus chihuahuensis*), mientras que encino azul (*Q. oblongifolia*) y saucillo (*Q. viminea*) se suman a los 1300 metros. Una pequeña población de *Q. arizonica* se registró a 1490 metros, bajo las antenas del cerro El Sainito, en tanto que encino roble (*Q. tuberculata*) se encuentra principalmente en los barrancos y cañadas de la transición del matorral espinoso al bosque de encino. En el borde oriental, cerca del Rancho El Berling, se tiene el único registro de *Q. perpallida* en la Sierra de Mazatán.

La vegetación de galería se encuentra restringida a los barrancos profundos y sombreados que descienden de la montaña, donde este tipo de vegetación alcanza los 1300 metros al sur de la sierra. En la cañada Agua de Don Luis, además de encontrar varios elementos del bosque tropical caducifolio y del matorral espinoso de pié de monte, así como cascalosúchil (*Plumeria rubra*) y grandes árboles de tescalama (*Ficus petiolaris*), capulín (*F. pertusa*), y guásima (*Guazuma ulmifolia*). En la cañada El Carrizo encontramos plantas que son afines a las floras de selva baja caducifolia en la región del Río Mayo, como por ejemplo: *Ayenia jaliscana*, copalquín (*Hintonia latiflora*), jícama (*Ipomoea bracteata*), garabato (*Pisonia capitata*), frijoles saltarines (*Sebastiania pavoniana*) y palo zorrillo (*Senna atomaria*); y de la Sierra El Aguaje en la región de Guaymas como capulín o nacapule (*Ficus pertusa*), cerote de cochi (*Iresine latifolia*), y chuparrosas (*Justicia californica* y *J. candicans*).

Análisis florístico

Actualmente, la flora vascular de la Sierra de Mazatán contabiliza 626 plantas distribuidas en 384 géneros y 104 familias. Las familias con mayor número de especies son Asteraceae (77), Fabaceae (72), Poaceae (62), Euphorbiaceae (29), Malvaceae (25), Cactaceae (20), Convolvulaceae (19), Solanaceae (17), Acanthaceae (16), y Plantaginaceae (14), incluyendo 17 especies de helechos y plantas afines.

La lista de las plantas vasculares de la Sierra de Mazatán se presenta en el Apéndice 1, cada taxón en la lista incluye las observaciones de campo o ejemplares de herbario relacionadas, indicándose el apellido del colector, número de colecta o fecha de observación, así como la base de datos o colección donde se encuentran registradas o depositadas las ocurrencias que lo respaldan. Un listado actualizado puede ser consultado en línea a travé del portal de la Red de Herbarios del Noroeste de México (2017) presentando un acceso directo a los datos de las ocurrencias relacionadas con cada taxón.

Entre las plantas que son importantes para la conservación destacan seis especies de encino y siete especies que están bajo la protección del gobierno mexicano (Diario Oficial de la Federación, 2010): baviso (*Brahea aculeata*), palma blanca (*Sabal uresana*), saya (*Amoreuxia palmatifida*), cabezas de viejo (*Mammillaria standleyi* y *Coryphanta recurvata*), palo fierro (*Olneya tesota*), guayacán (*Guaiacum coulteri*), y palma de la virgen (*Dioon sonorense*), llamada localmente "peine", categorizada como en peligro de extinción y que viene a ser la población más norteña de una cícada en el mundo.

También se pueden considerar objetos de conservación: una cactácea enlistada en The IUCN Red List of Threatened Species (Goettsch 2013), *Echinocactus horizonthalonius* var. *nicholii*, estaba registrada en Sonora de la Sierra El Viejo en el municipio de Caborca, pero también se registró en 2012 dentro de la zona de estudio, en el matorral espinoso cerca de Mazatán y Nácori Grande. Un par de orquídeas terrestres, *Hexalectris spicata* var. *arizonica* y *Hexalectris warnockii*, son registros únicos para Sonora. También, destacan *Ipomoea scopulorum* y *Tigridia pavonia*, y unas cactáceas con flores rojas como *Echinocereus santaritensis* subsp. *bacanorensis*, una variedad meridional, que florece en el verano, y *Echinocereus klapperi*, una especie rara que sólo se conoce de aquí y cerca de la presa El Novillo en el municipio de Soyopa.

En relación a los endemismos, *Agave ocahui*, *Agave shrevei* subsp. *matapensis*, *Echinocereus klapperi*, *Cottsia linearis* y *Dioon sonorense* son endémicas al estado de Sonora, mientras que *Diospyros reinae* (Wallnofer 2015) y *Perityle reinana* (Turner 2006) son endemismos locales cuya distribución está restringida a la Sierra de Mazatán. Adicionalmente, hay dos especies que aún no han sido descritas: una de ellas es un nopal (*Opuntia*) de distribución estatal y una *Bursera* subarbustiva de distribución local que crece en el bosque de encino y es endémica a la Sierra de Mazatán.

Varias plantas son de importancia económica para la población local, por ejemplo, el chiltepín (*Capsicum annuum* var. *glabriusculum*), que se utiliza como un condimento picante en la cocina sonorense y tiene un precio de mercado relativamente alto. Agave (*Agave angustifolia*), usado para hacer "bacanora", un mescal muy sonorense. La guayabilla (*Acacia russelliana*), es un árbol tropical que en la actualidad se encuentra escasamente en la zona debido a que ha tenido un uso intensivo como poste para cercas y vigas de casas en los ranchos.

Algunas especies están restringidas a las laderas y al fondo de los barrancos de la sierra, incluyendo *Ficus petiolaris*, *Ficus pertusa*, *Celtis reticulata*, *Guazuma ulmifolia*, *Euphorbia cymosa*, *Sebastiania pavoniana*, y *Dioon sonorense*. Otras especies están restringidas a las áreas ribereñas de los bosques de encino en los lugares más altos, incluyendo *Salix taxifolia*, *Prunus serotina* y *Lotus alamosanus*. Entre las plantas que sólo se encuentran en el bosque de encino se incluyen *Roldana hartwegii*, *Tephrosia nicaraguensis*, *Tephrosia thurberi*, *Tagetes* spp., *Salvia iodantha*, *Dalea exserta*, *Loeselia glandulosa*, *Loeselia pumila*, y *Stevia serrata*, entre muchas otras más.

A causa de a la cría de ganado, los pastos son muy importantes para la región y en este trabajo se registraron 63 especies de gramíneas. En los claros del bosque de encino del rancho El Bachán, se registraron *Bothriochloa barbinodis*, *Bouteloua hirsuta*, *Chloris virgata*, *Echinochloa crus-galli*, *Eragrostis mexicana*, *E. pectinacea* var. *pectinacea*, *Heteropogon melanocarpus*, *Muhlenbergia arizonica*, *M. rigens*, *Setaria pumila* y *Zuloagaea bulbosa*. En el matorral espinoso de pié de monte se registraron *Aristida adscensionis*, *Bouteloua aristidoides*, *B. barbata* var. *barbata*, *B. diversispicula*, y *Dinebra panicea* subsp. *brachiata*. *Aristida ternipes* var. *ternipes*, y *Lasiacis ruscifolia* se encontraron en los barrancos.

Figura 3. Vegetación de la región de la Sierra de Mazatán, municipio de Ures, Sonora. (A) Matorral desértico sonorense, con *Parkinsonia microphylla* y *Olneya tesota*, al sur de Rancho Viejo. (B) Mezquital, con *Prosopis velutina*, *Acacia occidentalis* y *Havardia mexicana*, Rancho El Tarais, al este de Rancho Viejo.

Figura 3. Vegetación de la región de la Sierra de Mazatán, Sonora (continuación). (C) Matorral espinoso de pie de monte, con *Lysiloma divaricatum*, *Ipomoea arborescens*, *Fouquieria macdougalii*, *Acacia cochliacantha* y *Stenocereus thurberi*, al oeste de Mazatán, municipio de Mazatán. (D) Encinal, con *Quercus viminea*, *Q. oblongifolia*, *Nolina microcarpa* y *Opuntia sp. nov.*, Cañada El Yugo, Rancho El Bachán, municipio de Ures.
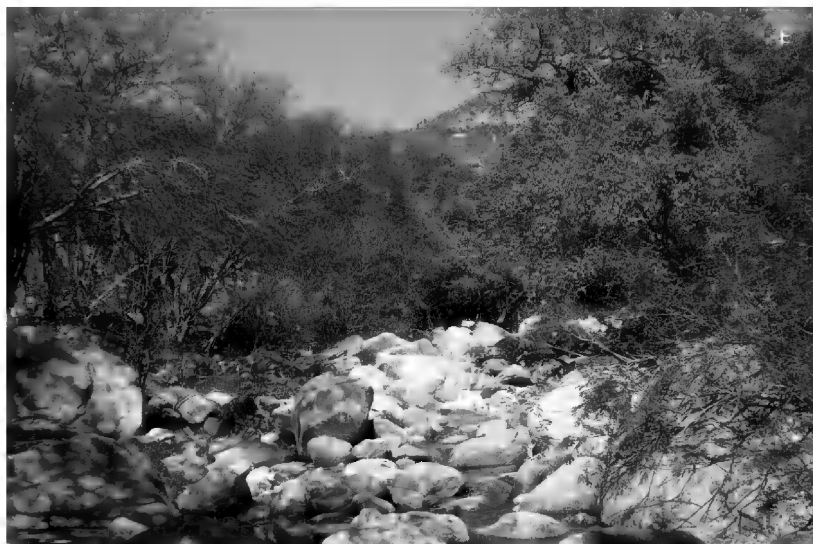
Figura 3. Vegetación de la región de la Sierra de Mazatán, Sonora (continuación). (E) Vegetación de galería, con *Vitex mollis*, *Guazuma ulmifolia*, *Lysiloma divaricatum* y *Caesalpinia pulcherrima*, al oeste de Mazatán, municipio de Mazatán. (F) Pastizal inducido en el encinal, con *Quercus chihuahuensis* y *Q. oblongifolia*. La planta con flores amarillas es *Viguiera lancifolia*, Rancho El Bachán, municipio de Ures.

Con respecto a los helechos y plantas afines, se registraron 18 especies en los géneros *Adiantum*, *Anemia*, *Asplenium*, *Astrolepis*, *Bommeria*, *Cheilanthes*, *Dryopteris*, *Myriopteris*, *Notholaena*, y *Pellaea*, así como una especie de *Selaginella*.

Las especies exóticas representaron el 6.13% de la flora. De las 38 especies no nativas registradas, *Pennisetum ciliare*, *Melinis repens*, *Cynodon dactylon*, *Avena fatua*, *Arundo donax*, *Lepidium didymum*, *Sorghum halepense*, *Ricinus communis*, *Parkinsonia aculeata*, *Polypogon monspeliensis*, *Sorghum halepense,* y *Nicotiana glauca* son las más importantes de tomar en cuenta debido a su naturaleza invasora.

CONCLUSIONES

Este listado florístico es muy importante no sólo para la Sierra de Mazatán, también lo es para la región central de Sonora. Sería una referencia de consulta obligada para la realización de estudios biológicos, ecológicos y sobre el aprovechamiento de las plantas nativas en esta región del estado. Hasta el momento, los resultados de este trabajo muestran una flora muy diversa, característica de tres ecosistemas, y el número de especies se incrementaría al llevarse a cabo exploraraciones en localidades y ambientes que hasta la fecha han sido poco recolectados. Es posible que, con colecciones adicionales, el número de especies podría alcanzar 700 taxa. Se recomienda recolectar los grupos de plantas que fueron poco muestreados durante este trabajo, principalmente las herbáceas de verano del matorral desértico sonorense y matorral espinoso; así mismo, las plantas de ambientes acuáticos y subacuáticos (arroyos, tinajas y represos) en el encinal y sobre las cañadas que descienden de la sierra. También, se recomienda una mayor exploración en localidades de la parte norte y este, así como el Cerro Prieto y cañadas como La Tigra, localizados en el extremo suroeste de la Sierra.

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Apéndice 1. Listado de las plantas vasculares de la Sierra de Mazatán, Sonora, México. Este listado está respaldado principalmente con los registros de ejemplares de herbario y observaciones de campo de los autores entre 2003 y 2015. Las especies no nativas se indican con un asterisco (*).

Cada taxón en la lista está respaldado con al menos un ejemplar de herbario u observación de campo cuyo registro puede ser consultado en el portal de la Red de Herbarios del Noroeste de México. Entre los paréntesis cuadrados se indican los herbarios donde se encuentran depositados los ejemplares, además de los nombres de las bases de datos en línea que contienen los registros de las observaciones de campo. Herbarios: USON = Universidad de Sonora; ARIZ = Universidad of Arizona; ASU = Arizona State University; NMC = New Mexico State University; SDSU = San Diego State University; MO = Missouri Botanical Garden; NY = New York Botanical Garden; MISSA = Mississippi State University; TEX = University of Texas. Bases de datos: Sonoran Atlas = Sonoran Desert Plants, an Ecological Atlas Database; MABA = Madrean Archipelago Biodiversity Assesment; RHNM = Red de Herbarios del Noroeste de México.

<div align="center">

HELECHOS Y PLANTAS AFINES

</div>

PTERIDOPHYTA

ANEMIACEAE
    Anemia tomentosa (Savigny) Sw. **var.** *mexicana* (C. Presl) Mickel
        Sánchez-E. 03-159 [USON]

ASPLENIACEAE
    Asplenium palmeri Maxon
        Sánchez-E. 04-078 [USON], Reina-G. 2004-1274 [USON]

DRYOPTERIDACEAE
    Dryopteris cinnamomea (Cav.) C. Christens.
        Sánchez-E. 05-048 [USON]
    Dryopteris knoblochii A.R. Sm.
        Sánchez-E. 03-305 [MO], Reina-G. 2004-1244 [USON]

PTERIDACEAE
    Adiantum poiretii Wikstr.
        Reina-G. 2004-1285 [USON]
    Astrolepis sinuata (Lag. ex Sw.) Benham & Windham
        Sánchez-E. 04-091 [USON]
    Astrolepis windhamii Benham
        Reina-G. 2004-1235 [MABA]
    Bommeria hispida (Mett. ex Kuhn) Underwood
        Sánchez-E. 03-158 [USON]
    Cheilanthes kaulfussii Kze.
        Sánchez-E. 03-221 [MO], Van Devender 2004-492 [MABA], Ferguson 2780 [MABA], Sánchez-
        E. 04-181 [USON], Sánchez-E. 03-307 [USON]
    Cheilanthes lozanoi **var.** *seemannii* (Hook.) Mickel & Beitel
        Sánchez-E. 2003-09-10 [RHNM]
    Myriopteris aurea (Poir.) Grusz & Windham
        Anderson 2004-13 [ASU], Sánchez-E. 03-220 [USON]
    Myriopteris lendigera (Cav.) Fée

Sánchez-E. 2015-03-20 [USON]
Myriopteris lindheimeri (Hook.) J. Sm.
    Van Devender 2004-493 [MO], Ferguson 2779 [MABA], Reina-G. 2004-1264 [MO], Van
    Devender 2014-04-27 [MABA]
Myriopteris pringlei **subsp.** *pringlei*
    Van Devender 2014-02-09 [MABA], Sánchez-E. 2013-011 [USON]
Myriopteris wrightii (Hook.) Grusz & Windham
    Sánchez-E. 04-004 [USON], Reina-G. 2015-03-20 [MABA]
Notholaena lemmonii **var.** *lemmonii*
    Reina-G. 2005-177A [MABA]
Pellaea ternifolia **subsp.** *arizonica* Windham
    Reina-G. 2005-218 [MABA], Sánchez-E. 03-308 [USON]

LICOPHYTA

SELAGINELLACEAE
Selaginella rupincola Underwood
    Sánchez-E. 03-146 [USON]

GIMNOSPERMAS

CONIFEROPHYTA

PINACEAE
Pinus herrerae Martínez
    Sánchez-E. 2014-04-29 [USON], cultivado en el rancho El Bachán.

CYCADOPHYTA

ZAMIACEAE
Dioon sonorense (De Luca, Sabato & Vázq. Torres) Chemnick, T.J. Greg. & Salas-Mor.
    Sánchez-E. 05-051 [USON]

ANGIOSPERMAS

MAGNOLIOPHYTA

DICOTILEDONEAS (MAGNOLIOPSIDA)

ACANTHACEAE
Anisacanthus andersonii T.F. Daniel
    Sánchez-E. 04-084 [USON], Hahn 36251 [USON]
Anisacanthus thurberi (Torr.) A. Gray
    Reina-G. 2014-02-08 [MABA]
Carlowrightia arizonica A. Gray
    Sánchez-E. 04-102 [USON]
Carlowrightia pectinata Brandegee
    Sánchez-E. 04-168 [USON]
Dicliptera resupinata (Vahl) Juss.
    Sánchez-E. 04-066 [USON]

Dyschoriste schiedeana **var.** *decumbens* (A. Gray) J. Henrickson
Sánchez-E. 03-316 [USON]
Elytraria imbricata (Vahl) Pers.
Van Devender 2011-06-22 [MABA], Sánchez-E. 03-246 [USON], Sánchez-E. 03-76 [USON]
Henrya insularis Nees ex Benth.
Hahn and Flesch 04-105 [NMC], Sánchez-E. 04-117 [USON]
Justicia californica (Benth.) D. Gibson
Sánchez-E. 04-134A [USON]
Justicia candicans (Nees) L. Benson
Sánchez-E. 04-098 [USON], Sánchez-E. 04-127 [USON], Sánchez-E. 05-030 [USON]
Justicia longii Hilsenb.
Reina-G. 2014-02-08 [MABA], Sánchez-E. 05-067 [USON]
Ruellia intermedia Leonard
Van Devender 2012-08-07 [MABA]
Ruellia nudiflora (Engelm. & A. Gray) Urban
Van Devender 2005-154 [USON]
Tetramerium abditum (Brandegee) T.F. Daniel
Van Devender 2004-482 [ASU], Sánchez-E. 04-045 [USON]
Tetramerium nervosum Nees
Sánchez-E. 03-127 [USON]
Tetramerium tenuissimum Rose
Van Devender 2012-386 [MABA], Reina-G. 2012-06-20 [MABA]

ACHATOCARPACEAE
Phaulothamnus spinescens A. Gray
Van Devender 2005-147 [USON], Sánchez-E. 05-070 [USON]

ADOXACEAE
Sambucus cerulea Raf.
Sánchez-E. 05-045 [USON], cultivado en el rancho El Álamo.

AMARANTHACEAE
Alternanthera stellata Uline et Bray.
Sánchez-E. 03-245 [USON], Sánchez-E. 03-121 [USON]
*Amaranthus albus L.
Sánchez-E. 03-238 [USON]
Amaranthus graecizans auct. non L.
Sánchez-E. 03-294 [USON]
Amaranthus palmeri S. Wats.
Sánchez-E. 04-109 [USON]
Chenopodiastrum murale (L.) S. Fuentes, Uotila & Borsch
Van Devender 2005-156A [SDSU], Reina-G. 2014-09 [SDSU]
Chenopodium neomexicanum Standl.
Van Devender 2011-06-22 [MABA], Sánchez-E. 03-118 [USON]
Dysphania ambrosioides (L.) Mosyakin & Clemants
Sánchez-E. 03-226 [USON], Sánchez-E. 05-015 [USON]
Gomphrena nitida Rothrock
Sánchez-E. 03-149 [USON]
Gomphrena sonorae Torr.
Sánchez-E. 03-138 [USON]

Guilleminea densa (Humb. & Bonpl. ex Willd.) Moq.
Reina G. 2004-1316 [USON]
Iresine latifolia Moq.
Sánchez-E. 05-019 [USON], Sánchez-E. 04-125 [USON], Sánchez-E. 04-198 [USON]
Monolepis nuttalliana (J.A. Schultes) Greene
Van Devender 2005-143 [ASU], Van Devender 2005-158 [NMC]
Tidestromia lanuginosa **var.** *eliassoniana* (Sánch. Pino & Flores Olv.) S.L. Welsh
Van Devender 2011-06-20 [MABA], Reina-G. 2014-02-08 [MABA]

ANACARDIACEAE
Rhus terebinthifolia Schltdl. & Cham.
Hahn 04-109 [USON]

APIACEAE
Daucus pusillus Michx.
Reina-G. 2005-175 [USON], Sánchez-E. 04-075 [USON]
Eryngium heterophyllum Engelm.
Sánchez-E. 03-156 [USON]
Eryngium nasturtiifolium Juss. ex Delar. f.
Sánchez-E. 04-137 [USON]

APOCYNACEAE
Asclepias angustifolia Schweig.
Van Devender 2004-472 [USON], Van Devender 2014-259 [MABA]
Asclepias elata Benth.
Enderson 2012-07-23 [MABA], Sánchez-E. 03-88 [USON], Sánchez-E. 03-125 [USON]
Asclepias lemmonii A. Gray
Reina-G. 2004-1226 [USON]
Cynanchum ligulatum (Benth.) Woods.
Van Devender 2011-10-20 [MABA]
Funastrum hartwegii (Vail) Schltr.
Van Devender 2015-03-21 [MABA]
Gonolobus arizonicus (A. Gray) Woods.
Reina G. 2004-1270 [MISSA]
Marsdenia edulis S. Wats.
Van Devender 2014-04-30 [MABA], Sánchez-E. 04-037 [USON]
Matelea tristiflora (Standl.) Woodson
Van Devender 2004-490 [USON], Enderson 2012-07-23 [MABA]
Metastelma latifolium J.N. Rose
Sánchez-E. 19115 [USON], Reina-G. 2005-190 [USON]
Pherotrichis schaffneri A. Gray
Reina-G. 2014-281 [MABA]
Plumeria rubra L.
Van Devender 2014-04-27 [MABA], Ferguson 2014-04-28 [MABA], Ferguson 2014-04-27 [MABA]
Polystemma canisferum McDonnell & Fishbein
Van Devender 2005-150 [USON]

ARALIACEAE
Aralia humilis Cav.

Sánchez-E. 03-231 [USON], Sánchez-E. 03-208 [USON], Hahn 34060 [USON]

ARISTOLOCHIACEAE
Aristolochia quercetorum Standl.
Reina-G. 2011-338 [MABA]
Aristolochia watsonii Woot. & Standl.
Reina-G. 2011-06-21 [MABA], Van Devender 2015-03-21 [MABA]

ASTERACEAE
Acourtia thurberi (A. Gray) Reveal & King
Sánchez-E. 03-150 [USON], Sánchez-E. 04-178 [USON]
Adenophyllum porophyllum **var.** *cancellatum* (Cass.) Strother
Reina-G. 2004-1209 [USON], Danforth 2008-09-25 [MABA]
Ageratum corymbosum Zuccagni
Sánchez-E. 03-302 [USON], Sánchez-E. 03-207 [USON]
Ambrosia ambrosioides (Cav.) W.W. Payne
Sánchez-E. 04-087 [USON], Van Devender 2011-06-22 [MABA]
Ambrosia confertiflora Dc.
Sánchez-E. 04-174 [USON], Sánchez-E. 03-113 [USON]
Ambrosia cordifolia (A. Gray) W.W. Payne
Sánchez-E. 04-160 [USON], Sánchez-E. 04-024 [USON], Sánchez-E. 2015-013 [USON]
Ambrosia monogyra (Torr. & A. Gray) Strother & B.G. Baldwin
Van Devender 2012-06-17 [MABA]
Artemisia ludoviciana Nutt.
Sánchez-E. 03-310 [USON]
Baccharis salicifolia (Ruiz & Pav.) Pers.
Reina-G. 2011-06-21 [MABA], Van Devender 2011-06-22 [MABA]
Baccharis sarothroides A. Gray
Van Devender 2011-10-20 [MABA]
Baccharis thesioides Kunth
Sánchez-E. 03-209 [USON], Reina-G. 2014-04-28 [MABA]
Bidens alba **var.** *radiata* (Sch. Bip.) R.E. Ballard
Sánchez-E. 03-298 [USON], Reina-G. 2004-1281 [USON]
Bidens aurea (Ait.) Sherff
Reina-G. 2004-1247 [USON]
Bidens bigelovii **var.** *angustiloba* (DC.) Ballard ex T.E. Melchert
Sánchez-E. 03-128 [USON], Reina-G. 2005-205 [USON]
Bidens pilosa L.
Sánchez-E. 03-217 [USON]
Brickellia baccharidea A. Gray
Van Devender 2004-1300 [USON], Van Devender 2014-04-27 [MABA], Reina-G. 2014-04-28 [MABA]
Brickellia betonicifolia A. Gray
Sánchez-E. 03-155 [USON], Sánchez-E. 03-269 [USON]
Brickellia coulteri A. Gray
Sánchez-E. 04-044 [USON], Van Devender 2004-487 [USON], Van Devender 2011-06-22 [MABA]
Brickellia eupatorioides (**var.** *chlorolepis* (Woot. & Standl.) B.L. Turner
Sánchez-E. 03-264 [USON]
Carminatia tenuiflora Dc.

Reina-G. 2004-1220 [USON]
Carphochaete bigelovii A. Gray
    Sánchez-E. 2015-03-20 [RHNM]
Chaetopappa ericoides (Torr.) G.L. Nesom
    Sánchez-E. 2005-04-26 [RHNM]
Conyza canadensis (L.) Cronq.
    Reina-G. 2004-1207 [USON]
Coreocarpus arizonicus (A. Gray) Blake
    Sánchez-E. 05-046 [USON], Reina-G. 2005-206 [USON]
Cosmos parviflorus (Jacq.) Pers.
    Sánchez-E. 03-199 [USON]
Diaperia verna (Rafinesque) Morefield
    Van Devender 2012-06-20 [MABA]
Eclipta prostrata (L.) L.
    Sánchez-E. 04-028 [USON], Sánchez-E. 04-033 [USON]
Encelia farinosa A. Gray ex Torr.
    Van Devender 2012-07-11 [MABA], Reina-G. 2014-02-08 [MABA]
Erigeron arisolius G.L. Nesom
    Sánchez-E. 03-278 [USON], Sánchez-E. 03-137 [USON]
Eupatorium collinum DC.
    Sánchez-E. 04-213 [USON], Sánchez-E. 04-085 [USON]
Fleischmannia sonorae (A. Gray) King & H.E. Robins.
    Reina-G. 2004-1246 [USON]
Galinsoga parviflora **var.** *parviflora*
    Sánchez-E. 05-004 [USON], Sánchez-E. 03-227 [USON]
Gamochaeta pensylvanica (Willd.) Cabrera
    Sánchez-E. 04-031 [USON], Sánchez-E. 2015-035 [USON]
Gamochaeta sphacelata (Kunth) Cabrera
    Sánchez-E. 04-069 [USON]
Gamochaeta stagnalis (I.M. Johnst.) Anderb.
    Reina-G. 2005-204 [USON], Sánchez-E. 05-047 [USON]
Guardiola platyphylla A. Gray
    Sánchez-E. 03-185 [USON], Anderson 2004-12 [ASU]
Heliomeris longifolia (Robins. & Greenm.) Cockerell
    Sánchez-E. 03-295 [USON]
Heterosperma pinnatum Cav.
    Sánchez-E. 03-321 [USON], Sánchez-E. 2009-165 [USON]
Laennecia eriophylla (A. Gray) G.L. Nesom
    Van Devender 2004-1309 [ASU]
Laennecia sophiifolia (Kunth) G.L. Nesom
    Sánchez-E. 03-230 [USON]
Lagascea decipiens **var.** *decipiens*
    Sánchez-E. 03-114 [USON], Sánchez-E. 03-123 [USON], Van Devender 2014-04-30 [MABA],
    Sánchez-E. 2013-005 [USON]
Lasianthaea fruticosa **var.** *occidentalis* K.M.Becker
    Sánchez-E. 03-133 [USON]
Logfia filaginoides (Hook. & Arn.) Morefield
    Sánchez-E. 2015-015 [USON]
Machaeranthera tagetina Greene
    Daniel 955 [ASU], Sánchez-E. 03-105 [USON]
Malacothrix clevelandii A. Gray

Sánchez-E. 2005-03-14 [RHNM]
Malacothrix sonorae W.S. Davis & Raven
Sánchez-E. 04-114 [USON], Sánchez-E. 2013-004 [USON], Van Devender 2005-233 [USON]
Melampodium longicorne A. Gray
Sánchez-E. 03-284 [USON]
Milleria quinqueflora L.
Sánchez-E. 03-161 [USON]
Parthenice mollis A. Gray
Van Devender 2012-08-07 [MABA]
Parthenium tomentosum var. *stramonium* (Greene) Rollins
T.R.Van Devender 2005-243 [NMC], Sánchez-E. 04-202 [USON]
Pectis filipes var. *filipes*
Sánchez-E. 03-313 [USON], Reina-G. 2004-1256 [USON]
Pectis prostrata Cav.
Reina-G. 2004-1261 [USON]
Pectis rusbyi Greene ex A. Gray
Sánchez-E. 2003-09-10 [RHNM]
Perityle californica Benth.
Sánchez-E. 04-038 [USON], Sánchez-E. 04-165 [USON], Sánchez-E. 2013-002 [USON]
Perityle microglossa Benth.
Sánchez-E. 04-036 [USON], Sánchez-E. 03-312 [USON], Van Devender 2005-237 [USON]
Perityle reinana B.L. Turner
Van Devender 2004-476 [ARIZ], Sánchez-E. 03-312 [USON], Sánchez-E. 04-048 [USON], Reina-G. 2004-1280 [MO]
Porophyllum gracile Benth.
Van Devender 2012-06-20 [MABA], Reina-G. 2014-02-08 [MABA]
Porophyllum pausodynum Robinson & Greenm.
Sánchez-E. 05-086 [USON]
Porophyllum macrocephalum DC.
Sánchez-E. 03-132 [USON]
Pseudognaphalium canescens (DC.) Anderb.
Sánchez-E. 03-317 [USON]
**Pseudognaphalium luteoalbum* (L.) Hilliard & Burtt
Sánchez-E. 2015-028 [USON]
Roldana hartwegii (Benth.) H.E. Robins. & Brett.
Danforth 2008-09-25 [MABA], Sánchez-E. 03-193 [USON], Sánchez-E. 03-154 [USON]
Stevia serrata Cav.
Sánchez-E. 03-325 [USON], Sánchez-E. 2009-164 [USON]
Tagetes lemmonii A. Gray
Sánchez-E. 2009-163 [USON], Sánchez-E. 03-213 [USON]
Tagetes micrantha Cav.
Sánchez-E. 2009-159 [USON], Sánchez-E. 2009-160 [USON], Sánchez-E. 03-291 [USON]
Tagetes subulata Cerv.
Sánchez-E. 2009-161 [USON], Sánchez-E. 03-140 [USON], Reina-G. 2004-1208 [USON]
Tagetes triradiata Greenm.
Sánchez-E. 2009-162 [USON], Sánchez-E. 03-218 [USON], Sánchez-E. 03-157 [USON], Reina-G. 2004-1208A [USON]
Thymophylla anomala Rydb.
Sánchez-E. 03-119 [USON], Reina-G. 2015-03-20 [MABA]
Thymophylla concinna (A. Gray) Strother
Sánchez-E. 04-101 [USON]

Thymophylla pentachaeta (DC.) Small
   Sánchez-E. 05-044A [USON]
Tithonia thurberi A. Gray
   Wiggins 357 [NY], Van Devender 2011-06-22 [MABA], Reina-G. 2011-06-21 [MABA], Van
   Devender 2011-10-20 [MABA]
Trixis californica **var.** *californica*
   Reina-G. 2005-231 [USON], Van Devender 2014-02-09 [MABA], Sánchez-E. 04-157 [USON],
   Sánchez-E. 04-112 [USON], Sánchez-E. 05-025 [USON]
Viguiera dentata (Cav.) Spreng.
   Sánchez-E. 03-296 [USON], Sánchez-E. 05-087 [USON]
Wedelia greenmanii B.L. Turner
   Sánchez-E. 03-216 [USON]
Xanthisma spinulosum (Pursh) D.R. Morgan & R.L. Hartman
   Sánchez-E. 05-018 [USON], Reina-G. 2015-29 [MABA]
Xanthium strumarium L.
   Van Devender 2011-10-20 [MABA], Sánchez-E. 03-328 [USON]
Zinnia zinnioides (H.B.K.) Olorode & A.M Torres
   Van Devender 2014-02-09 [MABA]

BEGONIACEAE
   Begonia gracilis Vilmorin-Andrieux
      Van Devender 2004-1299 [USON]

BIGNONIACEAE
   *Tecoma stans (L.) Juss. ex Kunth
      Sánchez-E. 03-122 [USON], Van Devender 2014-02-09 [MABA], Hale 2014-04-27 [MABA],
      Reina-G. 2014-04-28 [MABA]

BIXACEAE
   Amoreuxia gonzalezii Sprague & Riley
      Van Devender 2012-434 [USON], Van Devender 2012-494A [USON]
   Amoreuxia palmatifida Moc. & Sessé ex DC.
      Sánchez-E. 03-82 [USON], Van Devender 2012-433 [USON], Reina-G. 2012-450 [USON]

BORAGINACEAE
   Cordia sonorae Rose
      Sánchez-E. 03-169 [USON], Sánchez-E. 35855 [USON], Hahn 04-114 [USON]
   Cryptantha barbigera (A. Gray) Greene
      Sánchez-E. 04-049 [USON], Sánchez-E. 04-164 [USON], Sánchez-E. 2013-001 [USON]
   Eucrypta chrysanthemifolia **var.** *bipinnatifida* (Torr.) Constance
      Van Devender 2005-152 [USON], Sánchez-E. 04-089 [USON]
   Heliotropium curassavicum L.
      Reina-G. 2011-337 [MABA]
   Johnstonella angustifolia (Torr.) Hasenstab & M.G. Simpson
      Sánchez-E. 04-146 [USON]
   Nama hispida A. Gray
      Sánchez-E. 04-052 [USON]
   Nama jamaicense L.
      Sánchez-E. 04-138 [USON], Sánchez-E. 04-073 [USON], Sánchez-E. 04-116 [USON]
   Pectocarya recurvata I.M. Johnston

Reina-G. 2005-177 [USON], Sánchez-E. 05-038 [USON]
Phacelia gentryi Constance
Sánchez-E. 04-090 [USON], Sánchez-E. 04-065 [USON], Sánchez-E. 04-162 [USON], Sánchez-E. 2013-003 [USON]
Tiquilia canescens (DC.) A. Richards.
Van Devender 2012-02-02 [MABA]

BRASSICACEAE
Descurainia pinnata (Walt.) Britt.
Van Devender 2005-235 [ASU], Van Devender 2011-06-22 [MABA], Van Devender 2005-139 [NMC], Sánchez-E. 05-002 [USON], Van Devender 2005-139 [USON], Van Devender 2005-235 [USON], Sánchez-E. 2013-012 [USON]
Dryopetalon runcinatum A. Gray
Sánchez-E. 05-017 [USON]
*****Hirschfeldia incana** (L.) Lagrèze-Fossat
Sanchez E. 04-134 [ASU], Sánchez-E. 04-134 [USON]
*****Lepidium didymum** L.
Reina-G. 2005-202 [ASU], Reina-G. 2005-202 [USON]
Lepidium lasiocarpum Nutt.
Sánchez-E. 04-062 [USON], Sánchez-E. 04-153 [USON]
*****Sinapis arvensis** L.
Reina-G. 2005-168 [USON]
*****Sisymbrium irio** L.
Van Devender 2012-38 [MABA], Sánchez-E. 04-070 [USON]
Tomostima cuneifolia (Nutt. ex Torr. & A. Gray) Al-Shehbaz, M. Koch & Jordan-Thaden
Reina-G. 2005-176 [USON]

BURSERACEAE
Bursera sp. Jacq. ex L.
Bursera sp. nov. (sin publicar). Especie nueva, arbustiva, endémica a la Sierra y que crece bajo los encinos; Sánchez-E. 03-92 [USON], Sánchez-E. 03-147 [USON]
Bursera fagaroides var. elongata McVaugh & Rzed.
Sánchez-E. 03-94 [USON], Sánchez-E. 03-109 [USON], Sánchez-E. 03-214 [USON]
Bursera lancifolia Engl.
Sánchez-E. 03-327 [USON], Sánchez-E. 03-93 [USON]
Bursera laxiflora S. Wats.
Sánchez-E. 03-255 [USON], Sánchez-E. 03-63 [USON], Sánchez-E. 03-147 [USON], Sánchez-E. 03-100 [USON]

CACTACEAE
Carnegiea gigantea (Engelm.) Britton & Rose
Villa 2014-04-29 [MABA], Villa 2014-04-29 [MABA], Villa 2014-04-29 [MABA], Villa 2014-04-29 [MABA], Sánchez-E. 2004-10-09 [RHNM]
Coryphantha recurvata (Engelm.) Britt. & Rose
Van Devender 2011-350 [MABA], Enderson 2012-07-23 [MABA]
Cylindropuntia fulgida (Engelm.) Knuth
Van Devender 2011-06-22 [MABA]
Cylindropuntia leptocaulis (DC.) Knuth
Reina-G. 2014-02-08 [MABA], Reina-G. 2014-02-08 [MABA], Reina-G. 2014-02-08 [MABA], Sánchez-E. 2005-04-26 [RHNM]

Cylindropuntia thurberi (Engelm.) F.M. Knuth in Backeb. & F.M. Knuth
   Sánchez-E. 05-057 [USON], Villa 2014-04-27 [MABA], Reina-G. 2014-04-28 [MABA], Van Devender 2014-04-30 [MABA]
Cylindropuntia versicolor (Engelm. Ex J.M. Coult.) Knuth
   Reina-G. 2014-02-08 [MABA], Reina-G. 2014-02-08 [MABA]
Echinocactus horizonthalonius **var.** *nicholii* L. Benson
   Reina-G. 2012-149 [MABA], Van Devender. 2012-06-26 [MDE]
Echinocereus klapperi W. Blum
   Marc A. Baker 15878 [ASU], Reina-G. 2005-205B [MABA]
Echinocereus rigidissimus **var.** *rigidissimus*
   F. Molina-Freaner 2010-05-05 [MABA], Danforth 2014-04-27 [MABA], Van Devender 2014-04-27 [MABA], Reina-G. 2014-04-28 [MABA], Van Devender 2014-04-30 [MABA], Ferguson GMF 3551 [MABA], S.L. Minter 2014-04-27 [MABA], Sánchez-E. 05-053 [USON]
Echinocereus santaritensis **subsp.** *bacanorensis* W. Rischer & D. Felix
   Baker 15880 [SEINet], Minter 2014-07-28 [MABA], Enderson 2012-07-23 [MABA], Enderson 2012-07-23 [MABA]
Mammillaria grahamii **subsp.** *grahamii*
   Reina-G. 2014-02-08 [MABA], Van Devender 2005-133 [USON]
Mammillaria mainiae K. Brandeg.
   Van Devender 2005-134 [USON]
Mammillaria standleyi Orcutt.
   Molina-F. 2010-05-05 [MABA]
Opuntia sp. P. Mill.
   Opuntia sonorensis sp. nov. (unpublished, R. Puente).; Baker 15703 [SEINet], Van Devender 2004-499 [ASU], Van Devender 2004-481 [ASU]
Opuntia chlorotica Engelm. & Bigelow
   Van Devender 2014-02-09 [MABA], Van Devender 2014-04-27 [MABA], Rorabaugh 2014-04-29 [MABA], Reina-G. 2014-04-28 [MABA]
Opuntia engelmannii Salm-Dyck
   Rorabaugh 2014-04-29 [MABA], Ferguson 2014-04-29 [MABA]
Opuntia gosseliniana A. Weber
   Sánchez-E. 05-056 [USON]
Opuntia pubescens Wendl.
   Van Devender 2011-06-22 [MABA], Van Devender 2011-06-22 [MABA], Van Devender 2005-153 [USON], Sánchez-E. 2005-03-14 [RHNM]
Opuntia wilcoxii Britton & Rose
   Van Devender 2011-06-22 [MABA]
Pachycereus pecten-aboriginum Britton & Rose
   Van Devender 2011-06-22 [MABA]
Stenocereus alamosensis (J.M. Coult.) A.C. Gibson & K.E. Horak
   Reina-G. 2014-02-08 [MABA], Reina-G. 2014-02-08 [MABA], Van Devender 2014-04-30 [MABA]
Stenocereus thurberi (Engelm.) Buxbaum
   Van Devender 2011-06-22 [MABA]

CAMPANULACEAE
Lobelia endlichii (F. Wimmer) T.J. Ayers
   Van Devender 2004-477 [USON], Sánchez-E. 2015-03-20 [USON]
Lobelia laxiflora Kunth
   Van Devender 2014-04-29 [MABA], Hale 2014-04-28 [MABA]

CANNABACEAE
Celtis pallida var. pallida
Van Devender 2011-06-22 [MABA], Van Devender 2011-06-22 [MABA], Van Devender 2011-06-22 [MABA], Observador Desconocido 1971-07-00 [Sonoran Atlas], Reina-G. 2012-06-20 [MABA]
Celtis reticulata Torr.
Villa 2014-04-29 [MABA], Van Devender 2014-04-27 [MABA], Sánchez-E. 04-133 [USON], Sánchez-E. 05-022 [USON]

CARYOPHYLLACEAE
Drymaria laxiflora Benth.
Reina-G. 2005-205 [USON], Sánchez-E. 2015-03-20 [USON]
*Herniaria hirsuta **subsp.** *cinerea* (DC.) Coutinho
Reina-G. 2015-03-20 [MABA]

CISTACEAE
Lechea tripetala Britton
Sánchez-E. 05-054 [USON]

CLEOMACEAE
Cleome guianensis Aubl.
Reina-G. 2004-1307 [USON]
Polanisia dodecandra (L.) DC.
Sánchez-E. 05-076 [USON]

CONVOLVULACEAE
Cuscuta americana Thunb. ex Engelm.
Van Devender 2011-06-22 [MABA]
Cuscuta vandevenderi Costea & Stefanovic
Reina-G. 2004-1224 [USON]
Evolvulus alsinoides **var.** *angustifolia* Torr.
Van Devender 2011-06-22 [MABA], Sánchez-E. 03-250 [USON], Sánchez-E. 04-051 [USON], Sánchez-E. 04-166 [USON]
Evolvulus arizonicus A. Gray
Sánchez-E. 04-184 [USON]
Evolvulus filipes Mart.
Van Devender 2004-1306 [USON]
Ipomoea arborescens Sweet
Van Devender 2011-06-22 [MABA], Sánchez-E. 03-233 [USON]
Ipomoea bracteata Wight
Sánchez-E. 05-075 [USON], Sánchez-E. 04-126 [USON]
Ipomoea costellata Torr.
Reina-G. 2004-1241 [ARIZ], Reina-G. 2004-1241 [USON]
Ipomoea cristulata Hallier f.
Sánchez-E. 03-330 [USON]
Ipomoea longifolia Benth.
Reina-G. 2014-04-28 [MABA], Enderson 2012-07-23 [MABA]
Ipomoea pedicellaris Benth.
Sánchez-E. 2003-09-10 [RHNM]

Ipomoea purpurea (L.) Roth
Reina-G. 2044-1221 [USON]
Ipomoea scopulorum Brandegee
Van Devender 2014-367 [MABA]
Ipomoea ternifolia **var.** *leptotoma* (Torr.) J.A. McDonald
Van Devender 2012-06-17 [MABA]
Jacquemontia agrestis (Mart. ex Choisy) Meisn.
Sánchez-E. 03-91 [USON], Sánchez-E. 2003-09-10 [RHNM]
Jacquemontia pringlei A. Gray
Sánchez-E. 2003-09-10 [RHNM]
Merremia palmeri Hallier f.
Reina-G. 2014-02-08 [MABA], Reina-G. 2014-02-08 [MABA], Sánchez-E. 05-080 [USON]
Operculina pteripes (G. Don) O'Donell
Enderson 2012-07-23 [MABA], Sánchez-E. 03-148 [USON]

CRASSULACEAE
Crassula connata (Ruiz & Pav.) Berger
Sánchez-E. 05-040 [USON], Reina-G. 2015-03-20 [MABA]

CUCURBITACEAE
Cucurbita argyrosperma **var.** *palmeri* (L.H. Bailey) Merrick & D.M. Bates
Reina-G. 2011-06-21 [MABA], Van Devender 2011-10-20 [MABA]
Cucurbita digitata A. Gray
Sánchez-E. 05-079 [USON]
Echinopepon wrightii (A. Gray) S. Wats.
Van Devender 2011-06-22 [MABA]
Ibervillea sonorae Greene
Van Devender 2012-08-13 [MABA]
Melothria pendula L.
Sánchez-E. 03-290 [USON], Reina-G. 2004-1287 [USON]

EBENACEAE
Diospyros reinae B. Walln.
Hahn and Flesch 04-100 [NMC], Van Devender 2014-258 [MABA], Reina-G. 2004-1313 [ARIZ],
Reina-G. 2014-284 [MABA]

ELATINACEAE
Elatine brachysperma A. Gray
Sánchez-E. 2015-023 [USON]

EUPHORBIACEAE
Acalypha aliena Brandegee
Sánchez-E. 24167 [USON]
Acalypha californica Benth.
Van Devender 2004-484 [USON]
Acalypha neomexicana Muell.-Arg.
Sánchez-E. 03-228 [USON], Sánchez-E. 03-320 [USON]
Acalypha papillosa Rose
Sánchez-E. 2005-06-25 [RHNM]
Cnidoscolus angustidens Torr.

Enderson 2012-07-23 [MABA]

Croton alamosanus Rose
   Sánchez-E. 04-056 [USON]

Croton ciliatoglandulifer Ortega
   Reina-G. 2004-1206 [USON], Sánchez-E. 04-009 [USON]

Croton flavescens Greenm.
   Sánchez-E. 03-167 [USON], Sánchez-E. 03-060 [USON]

Croton potsii (Klotzsch) Muell.-Arg.
   Van Devender 2012-07-12 [MABA], Van Devender 2012-08-08 [MABA]

Croton sonorae Torr.
   Sánchez-E. 04-054 [USON]

Dalechampia scandens Vell.
   Sánchez-E. 27454 [USON], Sánchez-E. 05-012 [USON]

Ditaxis neomexicana (Muell.-Arg.) Heller
   Sánchez-E. 04-057 [USON]

Euphorbia albomarginata Torr. & A. Gray
   Reina-G. 2014-02-08 [MABA]

Euphorbia capitellata Engelm.
   Van Devender 2005-136A [USON]

Euphorbia cymosa Poir.
   Hahn and Flesch 04-103 [NMC], Villa 2014-04-29 [MABA], Van Devender 2014-04-30 [MABA]

Euphorbia heterophylla L.
   Sánchez-E. 03-271 [USON], Sánchez-E. 03-222 [USON], Reina-G. 2004-1215 [USON]

Euphorbia hirta L.
   Sánchez-E. 03-237 [USON], Sánchez-E. 03-219 [USON], Sánchez-E. 04-156 [USON]

Euphorbia hyssopifolia L.
   Sánchez-E. 03-294-a [ARIZ], Van Devender 2012-08-13 [MABA]

Euphorbia indivisa (Engelm.) Tidestr.
   Sánchez-E. 03-223 [USON]

Euphorbia setiloba Engelm. ex Torr.
   Reina-G. 2005-180 [USON]

Euphorbia subreniformis S. Wats.
   Sánchez-E. 03-319 [USON], Reina-G. 2004-1216 [USON]

Jatropha cardiophylla (Torr.) Muell.-Arg.
   Van Devender 2011-06-22 [MABA]

Jatropha cordata (Ortega) Müll. Arg.
   Van Devender 2011-06-22 [MABA]

Manihot angustiloba (Torr.) Müll. Arg.
   Sky Jacobs 2014-07-28 [RHNM]

*Ricinus communis L.
   Van Devender 2011-10-20 [MABA], Sánchez-E. 04-136 [USON]

Sebastiania bilocularis S. Wats.
   Sánchez-E. 04-058 [USON]

Sebastiania pavoniana (Müll. Arg.) Müll. Arg.
   Gentry 1957-05-12 [ARIZ], Sánchez-E. 04-040 [USON], Sánchez-E. 03-170 [USON]

FABACEAE

Acacia angustissima var. *filicioides* (Cav.) Kuntze
   Sánchez-E. 03-124 [ARIZ], Sánchez-E. 03-124 [USON]

Acacia cochliacantha Humb. & Bonpl. ex Willd.
   Sánchez-E. 03-257 [USON], Van Devender 2011-06-22 [MABA]

Acacia constricta Benth.
Reina-G. 2014-02-08 [MABA], Reina-G. 2014-02-08 [MABA], Reina-G. 2014-02-08 [MABA], Sánchez-E. 05-069 [USON]
Acacia farnesiana (L.) Willd.
Van Devender 2011-06-22 [MABA], Sánchez-E. 05-089 [USON], Reina-G. 2005-212 [USON], Sánchez-E. 03-139 [USON]
Acacia greggii A. Gray
Sánchez-E. 05-059 [USON]
Acacia occidentalis Rose
Van Devender 2011-06-22 [MABA], Reina-G. 2005-160 [USON], Sánchez-E. 04-196 [USON]
Acacia pennatula Benth.
Sánchez-E. 04-172 [USON], Sánchez-E. 04-201 [USON]
Acacia russelliana (Britton & Rose) Lundell
Sánchez-E. 04-108 [USON]
Aeschynomene fascicularis Cham. & Schlecht.
Sánchez-E. 04-106 [USON]
Aeschynomene villosa Poir.
Van Devender 2004-1293 [USON]
Astragalus nuttallianus **var.** *austrinus* (Small) Barneby
Van Devender 2005-135 [NMC]
Brongniartia nudiflora S. Wats.
Sánchez-E. 05-035 [USON]
Caesalpinia pulcherrima (L.) Sw.
Van Devender 2011-06-22 [MABA], Sánchez-E. 03-173 [USON]
Calliandra eriophylla Benth.
Van Devender 2004-505 [USON], Van Devender 2012-06-20 [MABA]
Chamaecrista absus (L.) H.S. Irwin & Barneby
Sánchez-E. 03-136 [ARIZ]
Chamaecrista nictitans **var.** *pilosa* (Benth.) H.S. Irwin & Barneby
Sánchez-E. 03-107 [USON]
Coursetia caribaea **var.** *caribaea* (Jacq.) Lavin
Sánchez-E. 03-65 [USON], Reina-G. 2005-209 [USON]
Coursetia glandulosa A. Gray
Van Devender 2011-06-22 [MABA], Sánchez-E. 04-053 [USON]
Crotalaria pumila Ortega
Sánchez-E. 04-188 [USON], Sánchez-E. 03-314 [USON]
Crotalaria sagittalis L.
Reina-G. 2005-214 [USON]
Dalea albiflora A. Gray
Sánchez-E. 03-143 [ARIZ], J.E.... 03-326 [NMC], Sánchez-E. 03-143 [USON]
Dalea exserta (Rydb.) Gentry
Sánchez-E. 03-280 [ARIZ], Sánchez-E. 03-280 [USON]
Dalea mollis Benth.
Sánchez-E. 04-214 [USON]
Dalea pogonathera A. Gray
Van Devender 2012-06-20 [MABA]
Dalea pringlei **var.** *multijuga* Barneby
Sánchez-E. 05-032 [USON]
Dalea pulchra Gentry
Van Devender 2005-225 [NY], Reina-G. 2014-04-28 [MABA], Van Devender 2014-04-30 [MABA]

Desmodium cinerascens A. Gray
Sánchez-E. 04-173 [USON], Van Devender 2004-491 [USON], Sánchez-E. 03-181 [USON]
Desmodium psilocarpum A. Gray
Reina-G. 2004-1253 [USON]
Desmodium retinens Schlecht.
Anderson 2004-10 [ASU], Sánchez-E. 03-201 [USON]
Desmodium scopulorum S. Wats.
Sánchez-E. 03-131 [USON]
Diphysa suberosa S. Wats.
Sánchez-E. 3-108 [ARIZ], Hedgcock 2014-04-27 [MABA], Sánchez-E. 03-108 [USON]
Erythrina flabelliformis Kearney
Sánchez-E. 21610 [USON], Sánchez-E. 03-117 [USON]
Eysenhardtia orthocarpa (A. Gray) S. Wats.
Sánchez-E. 03-103 [USON]
Galactia wrightii A. Gray
Sánchez-E. 03-188 [USON]
Haematoxylum brasiletto Karst.
Van Devender 2012-06-20 [MABA], Sánchez-E. s.n. [USON]
Havardia mexicana Britton & Rose
Van Devender 2011-06-22 [MABA], Sánchez-E. s.n. [USON]
Havardia sonorae Britton & Rose
Sánchez-E. 04-005 [USON]
Indigofera jamaicensis Spreng.
Reina-G. 2005-182 [USON], Sánchez-E. 04-083 [USON]
Hosackia alamosana Rose
Sánchez-E. 04-083 [USON]
Lysiloma divaricatum (Jacq.) J.F. Macbr.
Sánchez-E. 03-95 [USON], Reina-G. 2014-02-08 [MABA], Van Devender 2014-04-27 [MABA]
Lysiloma watsonii Rose
Sánchez-E. 03-115 [USON]
Macroptilium atropurpureum (Moc. & Sessé ex DC.) Urban
Sánchez-E. 05-010 [USON]
Macroptilium gibbosifolium (Ortega) A. Delgado
Sánchez-E. 03-224 [USON]
Marina parryi (Torr. & A. Gray) Barneby
Reina-G. 2014-02-08 [MABA]
*Medicago polymorpha L.
Van Devender 2005-224 [USON]
*Medicago sativa L.
Van Devender 2011-10-20 [MABA]
*Melilotus albus Medik.
Sánchez-E. 05-078 [USON]
*Melilotus indica (L.) All.
Van Devender 2015-72 [MABA]
Mimosa dysocarpa Benth.
Van Devender 2004-507 [USON], Sánchez-E. 03-111 [USON]
Mimosa laxiflora Benth.
 Van Devender 2011-06-22 [MABA]
Nissolia schottii (Torr.) A. Gray
Van Devender 2005-155 [USON]
Olneya tesota A. Gray

Van Devender 2011-06-22 [MABA], Sánchez-E. 05-083 [USON]

*_Parkinsonia aculeata_ L.

Van Devender 2011-06-22 [MABA], Sánchez-E. 05-090 [USON], Sánchez-E. 04-170 [USON]

Parkinsonia florida (Benth. ex A. Gray) S. Wats.

Reina-G. 2011-06-21 [MABA], Reina-G. 2014-02-08 [MABA], Reina-G. 2005-161 [USON]

Parkinsonia microphylla Torr.

Van Devender 2004-508 [USON], Reina-G. 2014-02-08 [MABA], Sánchez-E. 05-081 [USON]

Parkinsonia praecox **subsp.** _praecox_

Sánchez-E. 05-082 [USON], Sánchez-E. 04-215 [USON], Van Devender 2011-06-22 [MABA], Reina-G. 2012-06-27 [MABA], Reina-G. 2012-06-20 [MABA]

Phaseolus acutifolius A. Gray

Sánchez-E. 03-324 [USON], Reina-G. 2004-1240 [USON]

Piscidia mollis Rose

Van Devender 2011-06-22 [MABA], Sánchez-E. 03-165 [USON]

*_Prosopis juliflora_ **var.** _glandulosa_ (Torr.) Cockerell

Reina-G. 2011-06-21 [MABA]

Prosopis juliflora **var.** _torreyana_ L. Benson

Reina-G. 2012-06-20 [MABA]

Prosopis velutina (Woot.) Sarg.

Sánchez-E. 05-088 [USON], Reina-G. 2011-340 [ARIZ]

Rhynchosia minima (L.) Dc.

Reina-G. 2011-06-21 [MABA]

Rhynchosia precatoria Dc.

Reina-G. 2004-1283 [USON], Sánchez-E. 03-160 [USON]

Senna atomaria (L.) H.S. Irwin & Barneby

Sánchez-E. 04-041 [USON]

Senna covesii (A. Gray) H.S. Irwin & Barneby

Sánchez-E. 04-100 [USON]

Senna hirsuta **var.** _glaberrima_ (M.E. Jones) H.S. Irwin & Barneby

Sánchez-E. 03-211 [USON]

Senna obtusifolia (L.) H.S. Irwin & Barneby

Vargas-S. 2012-09-01 [RHNM]

Senna pallida **var.** _shreveana_ H.S. Irwin & Barneby

Sánchez-E. 03-168 [USON], Sánchez-E. 03-251 [USON], Sánchez-E. 2013-007 [USON]

Sesbania herbacea (P. Mill.) McVaugh

Van Devender 2011-10-20 [MABA]

Tephrosia multifolia Rose

Reina-G. 2004-1260 [ASU], Van Devender 2004-1294 [NMC]

Tephrosia nicaraguensis Oerst.

Sánchez-E. 2003-09-10 [RHNM]

Tephrosia thurberi (Rydb.) C.E. Wood

Sánchez-E. 03-192 [USON]

Zornia reticulata Sm.

Sánchez-E. 03-144 [USON]

FAGACEAE

Quercus arizonica Sarg.

Ferguson GMF 3555 [MABA]

Quercus chihuahuensis Trel.

Anderson 2004-9 [ASU], Reina-G. 2004-1288 [ARIZ], Sánchez-E. 03-110 [NMC], Reina-G. 2004-1288 [NMC], Sánchez-E. 03-110 [USON]

Quercus oblongifolia Torr.
    Van Devender 2004-498 [NMC], Sánchez-E. 03-197 [NMC], Sánchez-E. 05-042 [USON], Sánchez-E. 04-186 [USON], Sánchez-E. 03-197 [USON]
Quercus perpallida Trel.
    Sánchez-E. 04-014 [NMC], Sánchez-E. 04-014 [USON]
Quercus tuberculata Liebm.
    Hahn and Flesch 04-94 [NMC], Sánchez-E. 03-189 [USON], Hahn 34425 [USON]
Quercus viminea Trel.
    Anderson 2004-11 [ASU], Anderson 2004-14 [ASU], Van Devender 2004-479 [NMC], Van Devender 2004-500 [NMC], Sánchez-E. 04-94 [USON], Sánchez-E. 03-196 [USON]

FOUQUIERIACEAE
Fouquieria macdougalii Nash
    Van Devender 2011-06-22 [MABA], Sánchez-E. 03-234 [USON], Van Devender 2005-157 [USON]
Fouquieria splendens Engelm.
    Reina-G. 2014-02-08 [MABA], Van Devender 2014-02-09 [MABA], Villa 2014-04-29 [MABA]

GENTIANACEAE
Zeltnera calycosa (Buckley) G. Mans.
    Sánchez-E. 04-183 [USON]

HYPERICACEAE
Hypericum moranense Kunth
    Sánchez-E. 03-206 [USON], Reina-G. 2004-1263 [USON]

KRAMERIACEAE
Krameria erecta Willd. ex J.A. Schultes
    Van Devender 2004-488 [USON], Reina-G. 2011-06-21 [MABA], Van Devender 2012-06-20 [MABA], Reina-G. 2014-02-08 [MABA]

LAMIACEAE
Hedeoma nana subsp. *nana* (Torr.) Briq.
    Sánchez-E. 04-111 [USON]
Hyptis albida Kunth
    Sánchez-E. 03-112 [USON], Van Devender 2014-04-30 [MABA], Sánchez-E. 04-131 [USON]
Monarda citriodora subsp. *austromontana* (Epling) Scora
    Sánchez-E. 2003-09-10 [RHNM]
Salvia iodantha Fernald
    Sánchez-E. 03-229 [USON]
Salvia lasiocephala Hook. & Arn.
    Sánchez-E. 03-106 [USON]
Salvia misella Kunth
    Sánchez-E. 03-273 [USON]
Salvia palmeri Greene
    Reina-G. 2004-1271 [USON]
Salvia setosa Fernald
    Sánchez-E. 04-072 [USON], Sánchez-E. 04-163 [USON]
Stachys coccinea Ortega
    Sánchez-E. 03-151 [USON], Sánchez-E. 03-300 [USON]

Vitex mollis Kunth
  Sánchez-E. 03-175 [USON], Sánchez-E. 03-56 [USON], Sánchez-E. 04-199 [USON]

LINDERNIACEAE
  Lindernia dubia (L.) Pennell
    Van Devender 2004-502 [ASU]

LOASACEAE
  Mentzelia aspera L.
    Sánchez-E. 03-70 [USON]
  Mentzelia multiflora (Nutt.) A. Gray
    Sánchez-E. 04-189 [USON]

LORANTHACEAE
  Psittacanthus sonorae (Watson) Kuijt
    Sánchez-E. 03-163 [USON]
  Struthanthus palmeri Kuijt
    Van Devender 2004-496 [NMC]

LYTHRACEAE
  Cuphea wrightii A. Gray
    Sánchez-E. 03-153 [USON]

MALPIGHIACEAE
  Callaeum macropterum (Moc. & Sesse ex DC.) D.M. Johnson
    Daniel 952 [ASU], Van Devender 2011-06-22 [MABA], Sánchez-E. 04-059 [USON]
  Cottsia californica (Benth.) W.R. Anderson & C. Davis
    Sánchez-E. 04-050 [USON]
  Cottsia linearis (Wiggins) W.R. Anderson
    Sánchez-E. 04-103 [USON]

MALVACEAE
  Abutilon abutiloides (Jacq.) Garcke ex Britt. & Wilson
    Van Devender 2011-06-22 [MABA], Sánchez-E. 04-025 [USON], Sánchez-E. 04-171 [USON]
  Abutilon incanum (Link) Sweet
    Van Devender 2011-06-22 [MABA], Sánchez-E. 04-097 [USON]
  Abutilon reventum S. Wats.
    Reina-G. 2011-06-21 [MABA], Van Devender 2012-06-17 [MABA]
  Anoda abutiloides A. Gray
    Reina-G. 2004-1257 [USON]
  Anoda cristata (L.) Schlecht.
    Sánchez-E. 03-79 [USON], Sánchez-E. 03-297 [USON]
  Ayenia filiformis S. Wats.
    Sánchez-E. 03-78 [USON]
  Ayenia jaliscana S.Watson
    Sánchez-E. 03-68 [USON], Sánchez-E. 03-89 [USON]
  Bastardiastrum cinctum (Brandegee) D.M. Bates
    Sánchez-E. 05-029 [USON]
  Ceiba acuminata Rose
    Van Devender 2011-06-22 [MABA], Sánchez-E. 03-129 [USON]

Gossypium thurberi Todaro
　　Sánchez-E. 03-212 [USON]
Guazuma ulmifolia Lam.
　　Sánchez-E. 03-171 [USON]
Herissantia crispa (L.) Briz.
　　Van Devender 2011-06-22 [MABA], Sánchez-E. 03-261 [USON], Sánchez-E. 2013-008 [USON],
　　Sánchez-E. 04-151 [USON]
Hermannia pauciflora S. Wats.
　　Reina-G. 2005-178 [ARIZ], Reina-G. 2005-178 [NMC]
Hibiscus acicularis Standl.
　　Sánchez-E. 03-101 [USON], Sánchez-E. 04-060 [USON], Hahn 04-113 [USON]
Hibiscus biseptus S. Wats.
　　Van Devender 2005-227 [USON], Reina-G. 2005-179 [USON]
Hibiscus coulteri Harvey ex A. Gray
　　Van Devender 2005-230 [USON], Reina-G. 2005-163 [USON]
*Malva parviflora L.
　　Reina-G. 2005-165 [USON]
Malvastrum coromandelianum (L.) Garcke
　　Van Devender 2011-1075 [MABA]
Sida abutifolia P. Mill.
　　Reina-G. 2011-06-21 [MABA], Reina-G. 2011-06-21 [MABA], Van Devender 2012-06-20
　　[MABA], Van Devender 2012-07-12 [MABA], Sánchez-E. 05-037 [USON]
Sida alamosana S.Watson ex Rose
　　Sánchez-E. 04-159 [USON], Sánchez-E. 2013-006 [USON]
Sida ciliaris L.
　　Sánchez-E. 2015-03-20 [USON]
Sida hyalina Fryxell
　　Sánchez-E. 04-092 [USON], Sánchez-E. 03-260 [USON]
Sida rhombifolia L.
　　Sánchez-E. 03-329 [USON]
Sphaeralcea coulteri (S. Wats.) A. Gray
　　Van Devender 2005-141 [USON]
Waltheria indica L.
　　Van Devender 2014-04-27 [MABA], Reina-G. 2014-04-28 [MABA], Van Devender 2014-04-30
　　[MABA]

MARTYNIACEAE
Proboscidea parviflora (Woot.) Woot. & Standl.
　　A. Meling 1538 [USON], Sánchez-E. 03-177 [USON]

MELIACEAE
*Melia azedarach L.
　　Van Devender 2015-03-21 [MABA]

MENISPERMACEAE
Cocculus diversifolius Dc.
　　Van Devender 2011-06-22 [MABA], Sánchez-E. 05-092 [USON]

MOLLUGINACEAE
Glinus radiatus (Ruiz & Pav.) Rohrb.

Reina-G. 2011-335 [MABA], Reina-G. 2014-251 [MABA]
Mollugo verticillata L.
Sánchez-E. 04-055 [USON]

MORACEAE
Ficus pertusa L.f.
Sánchez-E. 03-057 [USON], Reina-G. 2005-197 [USON], Sánchez-E. 05-049 [USON]
Ficus petiolaris subsp. *petiolaris*
Sánchez-E. 03-164 [USON], Sánchez-E. 04-047 [USON]
Morus microphylla Buckl.
Van Devender 2011-10-20 [MABA]

NYCTAGINACEAE
Allionia incarnata L.
Reina-G. 2014-02-08 [MABA], Reina-G. 2014-02-08 [MABA], Sánchez-E. 04-104 [USON]
Boerhavia coccinea P. Mill.
Reina-G. 2011-06-21 [MABA]
Boerhavia diffusa L.
Sánchez-E. 03-55 [USON]
Boerhavia erecta L.
Sánchez-E. 03-86 [NMC]
Commicarpus scandens (L.) Standl.
Van Devender 2011-06-22 [MABA], Sánchez-E. 04-180 [USON], Van Devender 2005-145 [USON]
Pisonia capitata (S. Wats.) Standl.
Sánchez-E. 04-128 [USON], Sánchez-E. 05-091 [USON]

OLEACEAE
Forestiera angustifolia Torr.
Van Devender 2012-385 2 [MABA]

ONAGRACEAE
Epilobium canum subsp. *latifolium* (Hook.) Raven
Sánchez-E. 03-301 [USON]
Eremothera chamaenerioides (A. Gray) W.L. Wagner & Hoch
Reina-G. 2005183 [NMC]
Gongylocarpus rubricaulis Cham. & Schlecht.
Reina-G. 2004-1206A [USON]
Ludwigia octovalvis (Jacq.) P.H. Raven
Sánchez-E. 04-187 [USON], Sánchez-E. 03-303 [USON]
Ludwigia peploides (Kunth) P.H. Raven
Danforth 2014-04-27 [MABA], Sánchez-E. 04-082 [USON]
Oenothera curtiflora W.L. Wagner & Hoch
Sánchez-E. 04-142 [USON]
Oenothera kunthiana (Spach) Munz
Sánchez-E. 04-120 [USON], Sánchez-E. 05-061 [USON], Sánchez-E. 04-210 [USON], Van Devender 2005-148 [USON]
Oenothera primiveris A. Gray
Van Devender 2005-149 [USON], Sánchez-E. 05-001 [USON]

OROBANCHACEAE
  Castilleja tenuiflora Benth.
    Sánchez-E. 04-206 [USON]
  Orobanche cooperi (A. Gray) Heller
    Sánchez-E. 03-315 [USON]

PAPAVERACEAE
  Argemone ochroleuca Sweet
    Hale 2014-04-28 [MABA], Van Devender 2014-04-30 [MABA], Sánchez-E. 04-074 [USON]
  Eschscholzia californica **subsp.** *mexicana* (Greene) C. Clark
    Reina-G. 2005-181 [USON], Sánchez-E. 04-074 [USON]

PASSIFLORACEAE
  Passiflora arizonica (Killip) D.H. Goldman
    Sánchez-E. 03-184 [USON]
  Passiflora bryonioides Kunth
    Reina-G. 2004-1225 [USON]
  Passiflora foetida **var.** *gossypiifolia* (Ham.) Mast.
    Sánchez-E. 24532 [USON]
  Turnera diffusa Willd. ex Schult.
    Van Devender 2012-07-12 [MABA]

PHRYMACEAE
  Erythranthe floribunda (Douglas ex Lindl.) G.L. Nesom
    Sánchez-E. 04-067 [USON], Reina-G. 2004-1266 [USON], Reina-G. 2014-261 (TEX)
  Erythranthe guttata (Fisch. ex DC.) G.L. Nesom
    Sánchez-E. 04-081 [USON]

PHYTOLACCACEAE
  Stegnosperma halimifolium Benth.
    Reina-G. 2012-06-19 [MABA]

PICRAMNIACEAE
  Alvaradoa amorphoides Liebm.
    Sánchez-E. 2005-02-03 [RHNM]

PLANTAGINACEAE
  Antirrhinum costatum Wiggins
    Sánchez-E. 04-096 [USON], Sánchez-E. 2013-010 [USON]
  Callitriche deflexa A. Braun ex Hegelm.
    Sánchez-E. 2015-03-20 [USON]
  Mecardonia procumbens (P. Mill.) Small
    Sánchez-E. 04-061 [USON], Sánchez-E. 04-027 [USON], Sánchez-E. 03-145 [USON]
  Nuttallanthus canadensis (L.) D.A. Sutton
    Sánchez-E. 04-079 [USON], Van Devender 2005-194 [USON], Sánchez-E. 05-042A [USON]
  Nuttallanthus texanus (Scheele) D.A. Sutton
    Reina-G. 2005-170 [USON]
  Penstemon dasyphyllus A. Gray
    Sánchez-E. 03-179 [USON]
  Penstemon parryi (A. Gray) A. Gray

Reina-G. 2005-162 [USON], Sánchez-E. 05-039 [USON]
Plantago ovata Forsk.
Van Devender 2012-06-20 [MABA], Sánchez-E. 04-115 [USON], Sánchez-E. 04-143 [USON]
Plantago virginica L.
Sánchez-E. 04-190 [USON]
Russelia sonorensis var. sonorensis
Hale 2014-04-28 [MABA], Sánchez-E. 05-031 [USON], Sánchez-E. 03-183 [USON], Reina-G. 2015-03-20 [MABA]
Schistophragma intermedia (A. Gray) Pennell
Sánchez-E. 03-162 [USON]
Scoparia montevidensis (Spreng.) R.E. Fries
Sánchez-E. 04-063 [USON]
Stemodia durantifolia var. durantifolia
Van Devender 2011-06-22 [MABA], Sánchez-E. 04-035 [USON], Sánchez-E. 04-068 [USON], Sánchez-E. 2015-03-20 [USON]
Veronica peregrina subsp. xalapensis (Kunth) Pennell
Van Devender 2011-06-22 [MABA], Sánchez-E. 04-191 [USON], Sánchez-E. 04-071 [USON], Sánchez-E. 04-086 [USON], Sánchez-E. 05-044 [USON]

PLUMBAGINACEAE
Plumbago zeylanica L.
Sánchez-E. 04-129 [USON]

POLEMONIACEAE
Ipomopsis sonorae (Rose) A.D. Grant
Sánchez-E. 04-076 [USON]
Ipomopsis thurberi (Torr. ex A. Gray) V.E. Grant
Sánchez-E. 03-323 [USON], Sánchez-E. 03-204 [USON]
Loeselia glandulosa (Cav.) G. Don
Sánchez-E. 03-210 [USON], Sánchez-E. 03-182 [USON]
Loeselia pumila Walp.
Sánchez-E. 05-033 [USON]

POLYGALACEAE
Polygala alba Nutt.
Sánchez-E. 04-205 [USON]
Polygala barbeyana Chod.
Sánchez-E. 2015-018 [USON]
Polygala glochidiata Kunth
Sánchez-E. 03-141 [USON], Reina-G. 2005-195 [USON]
Polygala macradenia A. Gray
Wiggins & Rollins 389 [MOBOT], Van Devender 2012-06-20 [MABA], Van Devender 2012-07-12 [MABA]

POLYGONACEAE
Antigonon leptopus Hook. & Arn.
Van Devender 2004-510 [USON]
Persicaria pensylvanica (L.) G. Maza
Sánchez-E. 03-283 [USON], Van Devender 2004-1290 [USON]
*__Polygonum argyrocoleon__ Steud. ex Kunze

Reina-G. 2014-246 [MABA]
Polygonum aviculare L.
Sánchez-E. 04-118 [USON]

PORTULACACEAE
Portulaca suffrutescens Engelm.
Reina-G. 2004-1269 [ARIZ], Sánchez-E. 03-81 [USON], Sánchez-E. 03-248 [USON], Reina-G. 2004-1269 [USON]
Portulaca umbraticola Kunth
Sánchez-E. 03-247 [USON]

PRIMULACEAE
Anagallis arvensis L.
Van Devender 2015-03-21 [MABA], Sánchez-E. 2015-03-20 [USON]
Anagallis minima (L.) Krause
Sánchez-E. 2015-03-20 [USON]
Jacquinia macrocarpa subsp. *pungens* (A.Gray) B. Ståhl
Sánchez-E. 30742 [USON], Sánchez-E. 03-174 [USON]

RANUNCULACEAE
Clematis drummondii Torr. & A. Gray
Van Devender 2011-10-20 [MABA], Sánchez-E. 05-071 [USON]
Clematis ligusticifolia Nutt.
Reina-G. 2004-1279 [USON]
Thalictrum fendleri Engelm. ex A. Gray
Sánchez-E. 03-318 [USON]

RESEDACEAE
Oligomeris linifolia (Vahl) J.F. Macbr.
Van Devender 2005-140 [USON]

RHAMNACEAE
Colubrina viridis (M.E. Jones) M.C. Johnst.
Sánchez-E. 2011-09-20 [RHNM]
Condalia correllii M.C. Johnston
Van Devender 2012-07-12 [MABA]
Condalia globosa var. *globosa*
Sánchez-E. 04-158 [USON], Sánchez-E. 04-105 [USON]
Condalia warnockii M.C. Johnston
Van Devender 2011-06-22 [MABA]
Gouania rosei Wiggins
Sánchez-E. 03-64 [USON], Sánchez-E. 04-161 [USON]
Karwinskia humboldtiana Zucc.
Sánchez-E. 04-010 [USON], Van Devender 2011-06-22 [MABA]
Ziziphus obtusifolia (Hook. ex Torr. & A. Gray) A. Gray
Van Devender 2011-06-22 [MABA]

ROSACEAE
Prunus serotina var. *virens* (Woot. & Standl.) McVaugh

Sánchez-E. 04-211 [USON], Anderson 2004-17 [ASU], Ferguson GMF 3557 [MABA], Van Devender 2014-260 [MABA], Sánchez-E. 2014-049 [USON]

RUBIACEAE
  Bouvardia ternifolia (Cav.) Schlecht.
    Sánchez-E. 03-281 [USON], Anderson 2004-15 [ASU]
  Cephalanthus salicifolius Humb. & Bonpl.
    Sánchez-E. 05-074 [USON], Van Devender 2014-04-30 [MABA]
  Chiococca petrina Wiggins
    Sánchez-E. 2015-03-20 [USON]
  Diodia teres Walt.
    Sánchez-E. 03-120 [USON]
  Galium proliferum A. Gray
    Sánchez-E. 04-110 [USON]
  Hintonia latiflora Bullock
    Sánchez-E. 04-042 [USON], Sánchez-E. 29281 [USON]
  Mitracarpus hirtus (L.) Dc.
    Sánchez-E. 25263 [USON], Sánchez-E. 03-90 [USON], Sánchez-E. 03-244 [USON]
  Randia laevigata Standl.
    Reina-G. 2012-424 [MABA]
  Randia obcordata S. Wats.
    Van Devender 2004-506 [USON], Sánchez-E. 04-113 [USON], Sánchez-E. 04-007 [USON], Sánchez-E. 04-145 [USON]
  Randia sonorensis Wiggins
    Sánchez-E. 03-99 [USON], Van Devender 2014-02-09 [MABA], Reina-G. 2014-04-28 [MABA]
  Randia thurberi S. Wats.
    Reina-G. 2004-1204 [USON]

RUTACEAE
  Esenbeckia hartmanii B.L. Rob. & Fernald
    Van Devender 2011-06-22 [MABA], Sánchez-E. 04-043 [USON], Sánchez-E. 04-195 [USON]
  Zanthoxylum fagara Sargent
    Sánchez-E. 03-259 [USON], Sánchez-E. 040-088 [USON]

SALICACEAE
  Populus fremontii S. Wats.
    Van Devender 2011-1074 [MABA], Sánchez-E. 2014-053 [USON]
  Salix gooddingii Ball
    Reina-G. 2014-248 [MABA], Van Devender 2014-04-30 [MABA], Ferguson GMF 3525 [MABA]
  Salix taxifolia Kunth
    Sánchez-E. 03-293 [USON]

SANTALACEAE
  Phoradendron californicum Nutt.
  Van Devender 2011-06-22 [MABA], Sánchez-E. 03-116 [USON], Sánchez-E. 04-200 [USON]
  Phoradendron serotinum subsp. *tomentosum* (DC.) Kuijt
    Ferguson GMF 3556 [MABA], Sánchez-E. 03-268 [USON]

SAPINDACEAE
  Cardiospermum corindum L.

Sánchez-E. 03-236 [USON], Sánchez-E. 03-166 [USON]
Dodonaea viscosa var. angustifolia (L.f.) Benth.
Sánchez-E. 05-020 [USON], Sánchez-E. 04-016 [USON]
Serjania palmeri S. Wats.
Reina-G. 2011-337 [MABA], Van Devender 2011-10-20 [MABA]

SAPOTACEAE
Sideroxylon occidentale (Hemsl.) T.D. Penn.
Sánchez-E. 04-006 [USON]

SCROPHULARIACEAE
Buddleja parviflora Kunth
Sánchez-E. 04-015 [USON], Sánchez-E. 05-041 [USON]
Buddleja sessiliflora Kunth
Anderson 2004-16 [ASU], Van Devender 2011-06-22 [MABA], Hahn 04-101 [USON]

SOLANACEAE
Capsicum annuum var. glabriusculum (Dunal) Heiser & Pickersgill
Sánchez-E. 05-005 [USON], Sánchez-E. 04-177 [USON]
Datura discolor Bernh.
Van Devender 2011-06-22 [MABA], Reina-G. 2005-185 [USON]
Datura inoxia P. Mill.
Van Devender 2014-04-27 [MABA]
Datura lanosa Bye
Sánchez-E. 03-203 [USON]
Lycium andersonii A. Gray
Sánchez-E. 04-012 [USON], Sánchez-E. 04-008 [USON], Sánchez-E. 2013-013 [USON]
Lycium berlandieri Dunal
Van Devender 2005-146 [USON]
*__Nicotiana glauca__ Graham
Van Devender 2011-06-22 [MABA], Sánchez-E. 04-094 [USON]
Nicotiana obtusifolia M. Martens & Galeotti
Van Devender 2011-06-22 [MABA], Sánchez-E. 03-85 [USON], Sánchez-E. 04-023 [USON]
Petunia parviflora Juss.
Van Devender 2011-06-22 [MABA], Van Devender 2011-10-20 [MABA]
Physalis acutifolia (Miers) Sandw.
Sánchez-E. 03-71 [USON], Sánchez-E. 03-263 [USON]
Physalis crassifolia var. crassifolia
Reina-G. 2004-1258 [ASU]
Physalis pubescens L.
Sánchez-E. 04-019 [USON]
Solanum adscendens Sendtner
Sánchez-E. 28185 [USON]
Solanum elaeagnifolium Cav.
Sánchez-E. 03-104 [USON]
Solanum lumholtzianum Bartlett
Reina-G. 2011-06-21 [MABA], Van Devender 2011-06-22 [MABA]
Solanum nigrescens Mart. & Gal.
Sánchez-E. 03-272 [USON]
Solanum tridynamum Dun.

Anderson 2004-8 [ASU], Van Devender 2011-06-22 [MABA], Sánchez-E. 04-030 [USON], Sánchez-E. 04-179 [USON], Sánchez-E. 04-095 [USON]

TALINACEAE
Talinum paniculatum (Jacq.) Gaertn.
Van Devender 2012-08-13 [MABA]

URTICACEAE
Parietaria floridana Nutt.
Sánchez-E. 04-119 [USON], Sánchez-E. 04-029 [USON]

VERBENACEAE
Aloysia gratissima (Gillies & Hook.) Troncoso
Van Devender 2004-480 [USON], Sánchez-E. 05-036 [USON]
Glandularia gooddingii (Briq.) Solbrig
Sánchez-E. 04-099 [USON]
Glandularia pulchella (Sweet) Troncoso
Sánchez-E. 04-139 [USON]
Glandularia pumila (Rydb.) Umber
Reina-G. 2005-167 [USON]
Lantana camara L.
Sánchez-E. 04-174 [USON], Reina-G. 2005-192 [USON], Sánchez-E. 03-130 [USON]
Lantana urticifolia Mill.
Sánchez-E. 03-74 [USON], Sánchez-E. 05-028A [USON], Sánchez-E. 04-147 [USON]
Phyla nodiflora (L.) Greene
Van Devender 2011-10-20 [MABA]
Priva aspera Kunth
Reina-G. 2004-1237 [NMC], Reina-G. 2004-1237 [USON]
Verbena pinetorum Moldenke
Sánchez-E. 03-200 [USON]

VITACEAE
Cissus tiliacea Kunth
Reina-G. 2004-1239 [ARIZ]
Vitis arizonica Engelm.
Sánchez-E. 04-217 [USON], Sánchez-E. 03-225 [USON]

ZYGOPHYLLACEAE
Guaiacum coulteri A. Gray
Van Devender 2011-06-22 [MABA]
Kallstroemia californica (S. Wats.) Vail
Sánchez-E. 19419 [USON]
Kallstroemia grandiflora Torr. ex A. Gray
Sánchez-E. 03-262 [USON]

MONOCOTILEDONEAS (LILIOPSIDA)

AMARYLLIDACEAE
Hymenocallis sonorensis Standl.
Sánchez-E. 2005-06-25 [RHNM]

ARECACEAE
    Brahea aculeata (Brandegee) H.E. Moore
        Sánchez-E. 04-011 [USON], Sánchez-E. 05-013 [USON]
    Brahea brandegeei (C. Purpus) H.E. Moore
        Ferguson GMF 3521 [MABA], Hale 2014-04-28 [MABA]
    Sabal uresana Trel.
        Sánchez-E. 05-028 [USON]

ASPARAGACEAE
    Agave angustifolia **var.** *angustifolia*
        Van Devender 2011-06-22 [MABA], Reina-G. 2014-02-08 [MABA], Reina-G. 2014-02-08
        [MABA], Van Devender 2014-04-30 [MABA]
    Agave ocahui Gentry
        Ferguson GMF 3525 [MABA], Hale 2014-04-27 [MABA], Sánchez-E. 2004-10-09 [RHNM]
    Agave palmeri Engelm.
        Ferguson GMF 3533 [MABA]
    Agave shrevei **subsp.** *matapensis* Gentry
        Enderson 2012-07-23 [MABA], Sánchez-E. 03-190 [USON]
    Dasylirion gentryi D.J. Bogler
        Van Devender 2014-02-09 [MABA], Ferguson 2014-04-28 [MABA], Ferguson 2014-04-27
        [MABA], Reina-G. 2014-04-28 [MABA], Van Devender 2014-04-30 [MABA]
    Dasylirion wheeleri S. Wats.
        Sánchez-E. 2003-09-18 [USON]
    Echeandia flavescens (J.A. & J.H. Schultes) Cruden
        Ferguson GMF 3553 [MABA], Van Devender 2004-1308 [USON]
    Milla biflora Cav.
        Sánchez-E. 03-142 [USON]
    Nolina matapensis Wiggins
        Ladera sur del Cerro Prieto. Matorral espinoso de pié de monte con *Sabal, Dasylirion, Russelia.*,
        escasa, source: De acuerdo a la información proporcionada por el Sr. Mariano Amaya, residente de
        Rancho Viejo, Municipio de Ures.
    Nolina microcarpa S. Wats.
        Sánchez-E. 04-080 [USON]

BROMELIACEAE
    Hechtia montana Brandegee
        Sánchez-E. 26-072 [USON]
    Tillandsia recurvata (L.) L.
        Danforth 2008-09-25 [MABA], Villa 2014-04-27 [MABA], Ferguson GMF 3529 [MABA],
        Sánchez-E. 03-178 [USON]

COMMELINACEAE
    Commelina dianthifolia Delile
        Sánchez-E. 03-135 [USON], Sánchez-E. 03-194 [USON]
    Commelina erecta L.
        Sánchez-E. 03-215 [USON], Sánchez-E. 03-270 [USON], Sánchez-E. 03-277 [USON]
    Tradescantia gentryi D.R. Hunt
        Sánchez-E. 03-205 [USON], Sánchez-E. 03-186 [USON]

CYPERACEAE
Carex chihuahuensis Mackenzie
Reina-G. 2005-199 [USON]
Carex praegracilis W. Boott
Sánchez-E. 05-048 [ARIZ]
Cyperus mutisii (Kunth) Griseb.
Reina-G. 2004-1217 [MABA]
Cyperus sphaerolepis Boeckl.
Sánchez-E. 03-322 [MABA]
Cyperus squarrosus L.
Sánchez-E. 03-252 [USON], Reina-G. 2004-1234 [USON]

IRIDACEAE
Nemastylis tenuis (Herbert) Benth.
Sánchez-E. 03-187 [USON]
Sisyrinchium cernuum (Bickn.) Kearney
Van Devender 2005-239 [NMC], Sánchez-E. 04-070 [USON], Sánchez-E. 04-185 [USON],
Sánchez-E. 04-208 [USON], Sánchez-E. 04-077 [USON]
Tigridia pavonia Ker Gawl.
Van Devender 2014-04-27 [MABA]

JUNCACEAE
Juncus bufonius L.
Sánchez-E. 04-209 [USON]

ORCHIDACEAE
Hexalectris spicata **var.** *arizonica* (S. Wats.) Catling & V.S. Engel
Wilson 2005-09-02 [MABA], Wilson 2005-10-02 [ASU]
Hexalectris warnockii Ames & Correll
Wilson 2008-09-08 [MABA]
Sacoila lanceolata (Aubl.) Garay
Sánchez-E. 2005-06-25 [USON]

POACEAE
Aristida adscensionis L.
Van Devender 2004-1297A [USON], Sánchez-E. 04-149 [USON]
Aristida schiedeana Trin. & Rupr.
Reina-G. 2005-207 [USON]
Aristida ternipes **var.** *gentilis* (Henr.) Allred
Reina-G. 2004-1249 [ARIZ], Reina-G. 2004-1259 [USON]
Aristida ternipes **var.** *ternipes*
Sánchez-E. 03-73 [USON], Sánchez-E. 03-253 [USON], Van Devender 2005-156 [USON]
Arundinella palmeri Vasey in Beal
Reina-G. 2004-1236 [ARIZ]
*Arundo donax L.
Van Devender 2011-10-20 [MABA]
*Avena fatua L.
Reina-G. 2005-159 [USON]
Bothriochloa barbinodis (Lag.) Herter
Reina-G. 2004-1248 [USON], Sánchez-E. 03-285 [USON]

Bouteloua aristidoides (Kunth) Griseb.
   Sánchez-E. 03-241 [USON]
Bouteloua barbata var. *barbata*
   Sánchez-E. 04-144 [USON], Reina-G. 2011-06-21 [MABA], Van Devender 2011-06-22 [MABA],
   Reina-G. 2014-02-08 [MABA]
Bouteloua curtipendula (Michx.) Torr.
   Van Devender 2012-06-20 [MABA]
Bouteloua diversispicula J.T. Columbus
   Van Devender 2014-04-27 [MABA], Sánchez-E. 05-084 [USON], Sánchez-E. 04-150 [USON]
Bouteloua hirsuta Lag.
   Sánchez-E. 03-265 [USON]
Bouteloua repens (Kunth) Scribn. & Merr.
   Van Devender 2012-08-07 [MABA], Van Devender 2012-08-07 [MABA]
Chloris virgata Sw.
   Sánchez-E. 03-266 [USON]
*Cynodon dactylon (L.) Pers.
   Sánchez-E. 04-204 [USON], Reina-G. 2005-215 [USON]
*Dactyloctenium aegyptium (L.) Willd.
   Beetle M-6824 [ARIZ], Beetle M-6818 [ARIZ], Sánchez-E. 03-54 [USON], Sánchez-E. 03-254
   [USON]
Dasyochloa pulchella (Kunth) Willd. ex Rydb.
   Reina-G. 2014-02-08 [MABA], Sánchez-E. 05-084 [USON]
Dichanthium annulatum (Forssk.) Stapf
   Van Devender 2011-1069 [ARIZ]
Digitaria ciliaris (Retz.) Koel.
   Reina-G. 2004-1210 [ARIZ]
Dinebra panicea subsp. *brachiata* (Steud.) P. M. Peterson & N. Snow
   Sánchez-E. 03-239 [USON]
Dinebra panicoides (J. Presl) P.M. Peterson & N. Snow
   Reina-G. 2004-1272 [USON]
*Echinochloa crus-galli (L.) Beauv.
   Van Devender 2004-1291 [USON], Sánchez-E. 03-287 [USON]
Enneapogon desvauxii Desv. ex Beauv.
   Van Devender 2012-02-02 [MABA]
*Eragrostis cilianensis (All.) Vign. ex Janchen
   Van Devender 2011-06-22 [MABA], Sánchez-E. 03-287 [USON]
Eragrostis intermedia A.S. Hitchc.
   Reina-G. 2004-1232 [USON]
Eragrostis mexicana subsp. *mexicana*
   Van Devender 2004-1295 [ARIZ], Van Devender 2004-1295 [USON], Sánchez-E. 03-275
   [USON]
Eragrostis pectinacea var. *pectinacea*
   Van Devender 2004-1303 [ARIZ], Sánchez-E. 03-331 [USON], Van Devender 2004-1303
   [USON], Van Devender 2004-1297B [USON], Sánchez-E. 03-267 [USON]
Festuca octoflora var. *octoflora*
   Van Devender 2005-241 [USON]
Heteropogon contortus (L.) Beauv. ex Roemer & J.A. Schultes
   Reina-G. 2004-1250 [ARIZ], Reina-G. 2004-1250 [USON]
Heteropogon melanocarpus (Ell.) Ell. ex Benth.
   Sánchez-E. 03-279 [USON]
Lasiacis ruscifolia Hitchcock ex Chase

Van Devender 2004-489 [NMC], Sánchez-E. 04-130 [USON], Sánchez-E. 04-175 [USON], Sánchez-E. 03-61 [USON], Sánchez-E. 04-122 [USON]

Melinis repens* subsp. *repens
Van Devender 2011-10-20 [MABA], Van Devender 2014-02-09 [MABA], Van Devender 2014-04-27 [MABA], Reina-G. 2014-04-28 [MABA]

Muhlenbergia arizonica Scribn.
Beetle 1981-08-19 [ARIZ], Sánchez-E. 03-289 [USON]

Muhlenbergia dumosa Scribn. ex Vasey
Reina-G. 2004-1238 [USON]

Muhlenbergia elongata Scribn. ex Beal
Reina-G. 2004-1268 [ARIZ], Reina-G. 2004-1268 [USON]

Muhlenbergia emersleyi Vasey
Van Devender 2004-1304 [ARIZ], Van Devender 2004-1304 [USON]

Muhlenbergia gooddingii Söderstrom
Reina-G. 2004-1251 [ARIZ]

Muhlenbergia microsperma (DC.) Trin.
Sánchez-E. 04-176 [USON]

Muhlenbergia pectinata C.O. Goodding
Beetle 1981-08-19 [ARIZ], Reina-G. 2004-1267 [ARIZ], Van Devender 2004-1267 [USON]

Muhlenbergia rigens (Benth.) A.S. Hitchc.
Van Devender 2004-1310 [ARIZ], Sánchez-E. 03-288 [USON], Van Devender 2004-1310 [USON]

Muhlenbergia sinuosa Swallen
Van Devender 2004-1297 [USON], Reina-G. 2004-1233 [ASU], Reina-G. 2004-1231 [ARIZ], Reina-G. 2004-1231 [USON]

Muhlenbergia texana Buckl.
Van Devender 2004-1292 [USON]

Panicum ghiesbreghtii E. Fourn. ex Hemsl.
Beetle M-6854 [ARIZ]

Panicum hallii Vasey
Reina-G. 2004-1276 [ARIZ]

Panicum hirticaule* var. *hirticaule
Beetle M-6821 [ARIZ], Van Devender 2012-08-07 [MABA], Reina-G. 2014-02-08 [MABA]

Panicum virgatum L.
Reina-G. 2005-208 [USON], Reina-G. 2004-1277 [USON]

Pennisetum ciliare* (L.) Link
Reina-G. 2004-1277 [ARIZ]

Phalaris minor* Retz.
Van Devender 2004-474 [USON], Van Devender 2004-474 [ASU], Van Devender 2004-474 [NMC]

Phragmites australis (Cav.) Trin. ex Steud.
Sánchez-E. 2004-1277 [USON]

Poa bigelovii Vasey & Scribn.
Van Devender 2004-242 [USON]

Polypogon monspeliensis* (L.) Desf.
Van Devender 2014-257 [MABA]

Schizachyrium cirratum (Hack.) Woot. & Standl.
Reina-G. 2004-1255 [ARIZ]

Schizachyrium condensatum Nees
Reina-G. 2004-1231A [USON]

Setaria liebmannii Fourn.

Van Devender 2011-06-22 [MABA], Sánchez-E. 03-58 [USON], Sánchez-E. 03-242 [USON]

Setaria macrostachya Kunth
Reina-G. 2012-06-19 [MABA]

Setaria parviflora (Poir.) Kerguélen
Bernal 1981-07-04 [ARIZ], Reina-G. 2004-1278 [ARIZ]

***Setaria pumila** (Poir.) Roemer & J.A. Schultes
Sánchez-E. 03-286 [USON]

Sorghastrum nutans (L.) Nash
Reina-G. 2004-1252 [USON]

***Sorghum halepense** (L.) Pers.
Van Devender 2011-10-20 [MABA], Van Devender 2012-08-07 [MABA], Van Devender 2012-08-07 [MABA]

Trachypogon spicatus (L.) Kuntze
Reina-G. 2004-1265 [USON]

Tripsacum dactyloides (L.) L.
Reina-G. 2004-1254-A [ARIZ]

Tripsacum lanceolatum Rupr. ex Fourn.
Reina-G. 2014-04-28 [MABA]

Urochloa fusca (Sw.) B.F. Hansen & Wunderlin
Van Devender 2012-383 [ARIZ]

Zuloagaea bulbosa (Kunth) Bess
Sánchez-E. 03-292 [USON]

PONTEDERIACEAE
Heteranthera limosa (Sw.) Willd.
Sánchez-E. 03-332 [USON]

TYPHACEAE
Typha domingensis Pers.
Sánchez-E. 2005-02-17 [USON], Van Devender 2014-04-30 [MABA]

XANTHORRHOEACEAE
***Aloe vera** (L.) Burm. f.
Reina-G. 2014-07 [MABA]

RANGO DE TOLERANCIA Y ABUNDANCIA
DE *CORYPHANTHA CHIHUAHUENSIS* (CACTACEAE)
EN EL ESTADO DE CHIHUAHUA, MÉXICO

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RESUMEN
El rango de tolerancia es un conjunto de variables bióticas y abióticas que marcan límites de confort para las especies vegetales. Muestran atributos que ayudan a identificar el nivel de integración de una comunidad y conservación de la biodiversidad. El objetivo del estudio fue determinar el rango de tolerancia biótico de *Coryphantha chihuahuensis* mediante la asociación vegetal a la que responde y estimar su abundancia. El estudio se basa en un trabajo de campo con 20 parcelas de 100 m^2 cada una, donde el eje central es una planta de *C. chihuahuensis*. Sobre este cuadrante se realizó un levantamiento de especies existentes (arbustos, hierbas, gramíneas y cactáceas) y la cuantificación de ejemplares de *C. chihuahuensis*. Se analizó el número de especies, géneros y familias; así como la probabilidad de presencia de cada una. Se utilizaron estadísticas descriptivas que ayudaron a determinar la media de abundancia de la especie. Florísticamente, se obtuvieron un total de 25 familias, 51 géneros y 70 especies. La mayor probabilidad de presencia fueron las arbustivas con un 40%, seguidas por gramíneas 21%, herbáceas 20% y cactáceas 18%. La estima de abundancia para *C. chihuahuensis* es de seis plantas por 100 m^2 con todos los puntos de estudio y tres plantas sin incluir los sitios con mayor presencia para evitar sesgo. La abundancia de la especie va de una a 23 plantas en cada parcela. Aparte de tener una distribución muy restringida, *C. chihuahuensis* se encuentra vulnerable debido a que su hábitat está siendo invadido por el desarrollo urbano de la ciudad de Chihuahua.

ABSTRACT
The tolerance range is a set of biotic and abiotic variables that set limits of comfort for plant species. They show attributes that help identify the level of community integration and conservation of biodiversity. The objective of the study was to determine the range of biotic tolerance of *Coryphantha*

chihuahuensis through the plant association to which it responds and to estimate its abundance. The study is based on field work with 20 plots of 100 m2 each, where the central axis is a *C. chihuahuensis* plant. On this quadrant we surveyed existing species (shrubs, grasses, herbaceous and cacti) and quantified *C. chihuahuensis* specimens. The number of species, genera, and families was analyzed as well as the probability of presence of each one. Descriptive statistics were used to help determine the average abundance of the species. Floristically, a total of 25 families, 51 genera, and 70 species were obtained. The highest probability was 40% for shrubs, followed by grasses 21%, herbaceous 20%, and cacti 18%. The abundance estimate for *C. chihuahuensis* was six plants per 100 m2 with all study points and three plants without including sites with greater presence to avoid bias. The abundance of the species ranges from 1 to 23 plants in each plot. Apart from its restricted distribution, *C. chihuahuensis* is vulnerable because its habitat is being invaded by urban development from the city of Chihuahua.

La estructura de una comunidad biológica está determinada por patrones espaciales de distribución, por la clase y número de individuos que forman las poblaciones. En ellas se distinguen tres aspectos fundamentales: composición, estratificación y límites. La asociación vegetal muestra un conjunto de características fisiográficas y climáticas específicas. Además, cada sitio cuenta con condiciones bióticas y abióticas particulares que marcan límites y por tanto un rango de confort para las especies vegetales. Si este rango de tolerancia se altera, los organismos sufren un estrés que puede llegar a su extinción (Sánchez et al. 2011). El análisis y clasificación vegetal señalan un conjunto de variables biofísicas particulares, cuyos atributos ayudan a identificar el nivel de integración de una comunidad (Sosa et al. 2006; Rocha-Loredo et al. 2010), lo que conlleva a la conservación de la biodiversidad (Hernández & Godínez 1994). México a pesar de estar catalogado entre los cinco países megadiverso del mundo, ocupa el tercer lugar entre los países con mayores tasas de deforestación. Es un país con gran variedad de ecosistemas, pero el diagnóstico de su riqueza en diversidad vegetal todavía es insuficiente, así como algunos inventarios carecen de buena estructura (Valenzuela et al. 2015). Los mismos autores señalaron que más del 50% del territorio mexicano se encuentra ocupado por ecosistemas áridos y semiáridos, muchos de ellos perturbados y fragmentados. Al respecto señalaron que llegan a modificarse hasta 50,000 ha de vegetación en estas zonas por año. Esto a causa del cambio de uso de suelo, sobrepastoreo, extracción de especies, expansión agrícola y ganadera, principalmente (Valenzuela et al. 2015; Villanueva et al. 2016). A lo que subrayan Valenzuela et al. (2015) la poca documentación a esta afectación a la diversidad y composición vegetal en estos ecosistemas del país.

Dichos ecosistemas se caracterizan por tener las condiciones restringidas de humedad disponible en el suelo, junto con una estación corta de precipitación al año (250 mm o menor) y largas horas de exposición solar (Sosa et al. 2006; Lara-Juárez et al. 2016). Dentro de las zonas áridas y semiáridas se desarrolla la familia Cactaceae endémica del Continente Americano (Hernández & Godínez 1994; Villanueva et al. 2015; Lara-Juárez et al. 2016). Su mayor riqueza se encuentra en México, principalmente en tipos de vegetación de Matorral Desértico Rosetófilo (MDR) (Hernández & Godínez 1994; Lara-Juárez et al. 2016). Estudios como los efectuados por López-Gómez et al. (2010) demostraron que en estos tipos de clima existe mayor abundancia de cactáceas en áreas con exposición sur, a pesar de que la orientación norte genera hasta seis veces mayor humedad, gracias a una menor radiación solar; lo que indica la necesidad de que esta familia es de larga duración de exposición solar (López-Gómez et al. 2010). Hernández & Godínez, (1994) y Villanueva et al. (2015) expusieron que los cactus son una de las familias más amenazadas, con un endemismo de hasta el 80% en el territorio mexicano. Villanueva et al. (2015) resaltaron el valor de estas plantas en el país debido a su impacto cultural, social, económico y ecológico, ya que han sido utilizadas en el sector alimenticio, medicinal, religioso, forrajero, así como cercos vivos, y plantas de ornato. Por tanto, son de las especies de planta más amenazadas por el comercio, la recolección ilegal, el cambio de uso de suelo y la industrialización.

El género *Coryphantha* es uno de los más diversos dentro de la familia con 60 o más taxones. Según Ditch & Luthy (2005) y Lebgue & Quintana (2013), a excepción de una franja pequeña en el suroeste de los Estados Unidos, la distribución del genero está prácticamente restringida en México, extendiéndose desde el este hasta el oeste, cubriendo las dos Sierras Madres (Sierra Madre Oriental y Sierra Madre Occidental), y ocupando áreas de los dos desiertos (Chihuahuense y Sonorense), desde el norte hasta el sur del país. Una de las especies poco estudiadas dentro de esta familia es *Coryphantha chihuahuensis* endémica del estado de Chihuahua en el Desierto Chihuahuense (Estrada-Castillo & Villarreal-Quintanilla 2010; Lebgue & Quintana 2013). Su hábitat es limitado y se presenta en forma de manchones dentro de los Matorrales Desérticos Micrófilos (MDM) y Matorrales Desérticos Rosetófilos (MDR) a altitudes de 1200 a 1700 msnm (Lebgue & Quintana 2013).

En un estudio realizado por Alanís-Rodríguez et al. (2015) se analizaron dos tipos de MDR con distintos tipo de suelo (Rendzina + Litosol, textura media, lítico y Regosol calcárico + Litosol, textura media) donde demostraron que, aunque sea el mismo tipo de vegetación, existen variaciones bióticas o abióticas que conllevan a la formación de distintas asociaciones vegetales.

El objetivo del estudio fue determinar el rango de tolerancia biótico de *Coryphantha chihuahuensis* mediante la asociación vegetal a la que responde y estimar su abundancia. Esto será de interés para especialistas en biología, científicos o tecnólogos que requieran saber sobre la distribución ecológica y su especiación en el estado de Chihuahua.

REVISIÓN DE LITERATURA

Tipos de Vegetación en Chihuahua

El estado de Chihuahua tiene con una superficie de 247,087 km^2. Dentro de su fisiografía, la región centro se caracteriza por estar dentro de dos provincias fisiográficas: Sierra Madre Occidental y Sierras y Llanuras del Norte. Estas últimas abarcan el 70% del territorio, representan las zonas áridas y semiáridas del estado (Estrada-Castillón & Villarreal-Quintanilla 2010; INAFED 2015; Consejo Nacional Forestal 2011; Gobierno del estado de Chihuahua 2015). A su vez, estas zonas ocupan el 34% del ecosistema Desierto Chihuahuense (DCh) (Estrada-Castillo & Villarreal-Quintanilla 2010), lugar donde se alberga parte de la región florística xerofítica de México, en donde sobresale la familia Cactaceae (Estrada-Castillón & Villarreal-Quintanilla 2010). El estado cuenta con matorral xerófilo, pastizal y bosque de encino-pino, principalmente (Rzedowski 2006). A lo que Lebgue & Quintana (2013) mencionaron que la vegetación hogar de las cactáceas son los matorrales desérticos micrófilos y rosetófilos, mezquitales, pastizales, bosques templados y bosques tropicales caducifolios.

Matorral Desértico o Xerófilo

El Matorral Desértico también conocido como Matorral Xerófilo se caracteriza por comunidades de porte arbustivo, adaptadas de climas áridos y semiáridos. Posee una gran diversidad de especies debido a la variedad de formas biológicas. El 32% de la superficie del estado de Chihuahua está ocupada por Matorrales Xerófilos (Lebgue & Quintana 2013). Esto contribuye a que la organización de algunas comunidades vegetales pueda llegar a ser muy sencillas. A su vez el endemismo encontrado en este tipo de vegetación es de una riqueza considerable (Rzedowski 2006). Cabe mencionar aquí que el Matorral Desértico o Xerófilo está formado por dos asociaciones vegetales que a continuación se describen brevemente:

Matorral Desértico Micrófilo y Rosetófilo

El aspecto fisonómico es el que identifica al Matorral Desértico Micrófilo (MDM), ya que se caracteriza por tener arbustos de hojas pequeñas, con o sin espinas. Estas agrupaciones son las más abundantes en las zonas áridas del estado inclusive del país y se ubican sobre planicies y lomeríos bajos. Dentro de las especies más sobresalientes están *Larrea tridentata, Flourensia cernua, Prosopis*

glandulosa, Fouquieria splendens, Parthenium incanum, Jatropha dioica, Cetlis pallida, Opuntia sp., entre otras (Rzedowski 2006; Lebgue & Quintana 2013).

Los Matorrales Desérticos Rosetófilos (MDR) son caracterizados por tener vegetación con hojas grasas agrupadas en forma de rosetas. Se ubican en las partes altas de los lomeríos provenientes de rocas ricas en carbonato de calcio. Estos tipos de matorrales se ubican desde el este de Chihuahua hasta San Luis Potosí (Rzedowski 2006; Estrada-Castillón & Villarreal-Quintanilla 2010; Lebgue & Quintana 2013). Las plantas más características son: *Agave lechuguilla, Dasylirion wheeleri, Yucca* sp., *Euphorbia antisiphylityca, Senna wislizenii, Tecoma stans, Aloysia wrightii,* entre otras. En ocasiones, es complicado hacer una delimitación precisa ya que las dos asociaciones vegetales llegan a compartir las mismas especies florísticas. Los dos tipos de matorrales antes mencionados; contienen el 65% de todas las especies de cactáceas encontradas en el estado de Chihuahua (Lebgue & Quintana 2013).

Figura 1. *Coryphantha chihuahuensis* en sitios de muestreo. Foto por I.K. Ibarra.

Hábitat de *Coryphantha chihuahuensis*

La distribución de *C. chihuahuensis* (Figura 1) es limitada. Fue recolectada por Palmer en 1908 en montañas a 20 km de la ciudad de Chihuahua, Chih. (Bravo-Hollis & Sanchez- Mejorada 1991; Anderson 2001). En estudios de campo como los realizados por Lebgue & Quintana (2013) reportaron a la especie en los alrededores de la ciudad de Chihuahua y municipios adyacentes de Delicias y Rosales. Los mismos autores mencionaron que la especie se desarrolla en tipo de vegetación de MDM y MDR; aparte de estas dos asociaciones vegetales no se conoce más sobre su distribución.

MATERIALES Y MÉTODOS

El trabajo de campo se llevó a cabo en los meses de julio y agosto de 2013. Se analizaron 20 puntos con presencia de *Coryphantha chihuahuensis* previamente registrados dentro del estado de Chihuahua, en los municipios de Chihuahua, Aldama, Aquiles Serdán, Rosales y Satevó (Figura 2; Tabla 1) (Ibarra-Díaz Velarde et al. 2016).
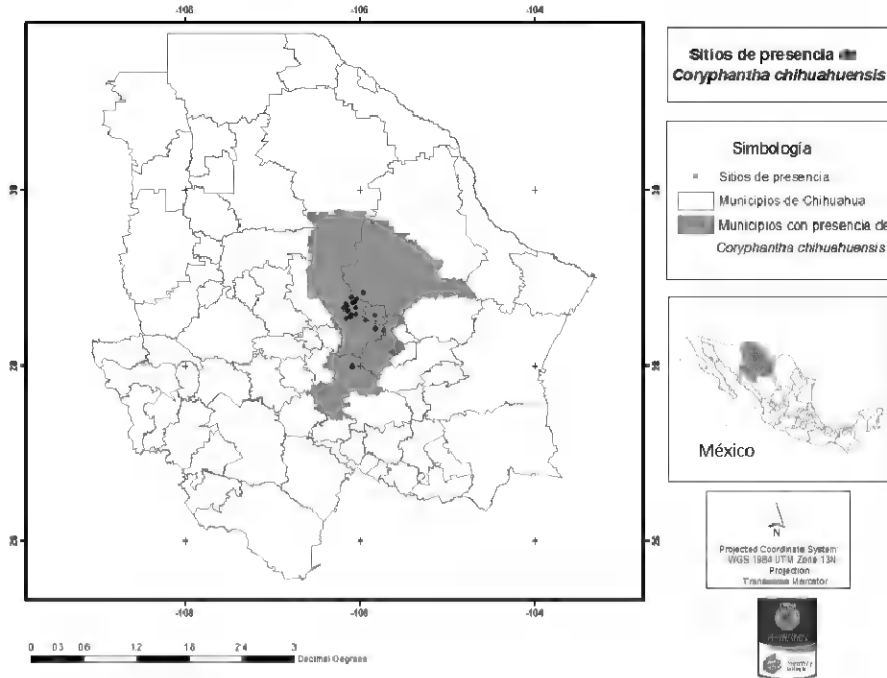
Figura 2. Ubicación de la zona de estudio y 20 parcelas.

En estos puntos se seleccionó una planta de *Coryphantha chihuahuensis* al azar, misma que se tomó como eje central para delimitar un cuadrante de 10 X 10 m (Fig. 3), medida utilizada por Figueroa & Giménez (2015) para registrar densidad de especies. Sobre este cuadrante se realizó un levantamiento de especies existentes y la cuantificación de ejemplares de *C. chihuahuensis*. De igual forma, se tomó registro de especies de: arbustos (Sp), herbáceas (H), gramíneas (Z) y presencia de otras cactáceas (C); así como los datos espaciales de altitud, orientación o exposición. A los sitios de muestreos se les dio una clasificación en torno a su ubicación: cercano a zona urbana; cercano a caminos ya sean carreteras, caminos o brechas; cercano a desarrollos carreteros o nuevos caminos y; zonas internas. Los parámetros a seguir para la zona urbana fueron: espacio rodeado de desarrollo urbano y la cercanía al mismo no mayor a 500 m. Cercano a carreteras o caminos: un máximo de 500 m del camino al punto de muestreo o que exista vista de la parcela al camino. Cercano a desarrollos carreteros: carreteras en construcción a una distancia máxima de 500 m de la carretera o camino. Zonas internas: puntos a más de 500 m de algún camino, asentamiento o desarrollo humano (Tabla 2).
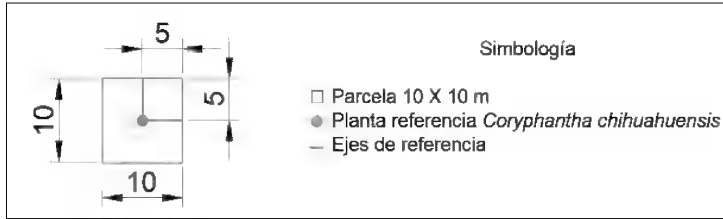
Figura 3. Modelo de parcela 10 X 10 m.

Análisis Estadísticos

Para determinar la sociabilidad vegetal de *Coryphantha chihuahuensis* se registraron las especies encontradas correspondientes a los grupos antes señalados, dentro de las parcelas de 10 X 10 m. Se elaboró una lista con los individuos por sitio. Se analizó el número de especies, género y familia; número total de especies por sitio; especies más frecuentes; como la probabilidad de presencia de cada una, se utilizó el programa Minitab 16. También, se utilizaron estadísticas descriptivas para determinar la media de abundancia de la especie. Para esto, utilizando Minitab 16 y Excel 2013, se realizaron dos cálculos: uno con el total de los registros y el otro sin considerar los tres sitios donde se registraron más abundancia poblacional de *C. chihuahuensis*; y esto para evitar algún sesgo.

RESULTADOS Y DISCUSIONES

Coryphantha chihuahuensis se desarrolla mayormente en el MDM (80%), ya que solo el 20% de las muestras fueron encontradas en las condiciones ambientales del MDR. Florísticamente, se obtuvieron en el área de estudio un total de 275 registros los cuales arrojaron 25 familias, 51 géneros, 71 especies incluyendo *C. chihuahuensis*. Según la forma de vida de las plantas, se encontraron 20 especies arbustivas (Tabla 4), 22 herbáceas (Tabla 5), 19 gramíneas (Tabla 6) y 10 suculentas (cactáceas) incluyendo *C. chihuahuensis* (Tabla 7). Aunque las herbáceas dominaron en diversidad, las arbustivas sobresalieron en abundancia. Estas últimas cuentan con 111 registros, seguidas de gramíneas con 58, herbáceas 56 y 50 cactáceas (incluyendo *C. chihuahuensis*) (Tabla 3). Las especies con mayor presencia son *Aloysia wrightii* (Sp4) y *Tecoma stans* (Sp18) registradas en los sitios 19 y 18, respectivamente; la arbustiva *Mimosa aculeatifolia* (Sp14) con 14 presencias; *Opuntia* sp. (C8) con 11 registró, seguidas de *Jatropha dioica* (Sp12) y *Sida procumbens* (H17) con 10 repeticiones cada uno. Con menor presencia se encuentra *Cenchrus ciliaris* (Z7) con 9, *Croton pottsii* (H5) y *Heteropogon contortus* (Z11) con 8 registros cada una.

Del total de las especies registradas, el 46.5% tienen presencia en un solo sitio; esto representa el 27.3% en arbustivas, el 36.4% de herbáceas, de gramíneas 24.2% y de cactáceas el 12.1%. Por otro lado, el 28.2% del total de las especies tienen presencia en 5 sitios o más. Las especies arbustivas repuntan en presencia con el 45%, seguida de las gramíneas con el 25%, las herbáceas y cactáceas con 15% cada una. Mientras que con 10 registros sólo se encuentran el 11.1% de las especies.

En cuanto a la probabilidad de presencia por formas de vida, las arbustivas representan un 40%, seguidas de las gramíneas y herbáceas con 21 y 20%, respectivamente y con menor probabilidad las cactáceas con un 18% (Tabla 3).

Al analizar los datos registrados, se detectó que C*oryphantha chihuahuensis* se asocia principalmente con *Aloysia wrightii* (Sp4) y *Tecoma stans* (Sp18) (95 y 90% de probabilidad de asociación); seguida por *Mimosa aculeatifolia* (Sp14) (70%); *Opuntia* sp. (C8) (55%); *Jatropha*

dioica (Sp12) (50%), *Sida procumbens* (H17) (50%), y *Celtis pallida* (Sp7) (45%), incluyendo dos gramíneas, *Cenchrus ciliaris* (Z7) y *Heteropogon contortus* (Z11) (45 y 40%). Dicha probabilidad de asociación se redujo para el resto de las especies encontradas en el área de estudio (35% o menos).

Por otro lado, la abundancia estimada de seis plantas de *Coryphantha chihuahuensis*/100 m^2, fue obtenida considerando a todos los sitios de muestreo; sin embargo, al eliminar los tres sitios con mayor concentración de individuos, esta abundancia se redujo a tres plantas/100 m^2. Dichos sitios con mayor población de *C. chihuahuensis* fueron el 8 con 23 plantas, el 2 con 19 y el sitio 19 con 11 plantas. El resto de los sitios presentaron poblaciones desde un individuo de planta hasta 7/100 m^2. La probabilidad de que existan de una a siete plantas en 100 m^2 es de 90%, mientras una población mayor a siete plantas es sólo del 20% (Tabla 8). Se podría asumir una diferencia de abundancia importante entre parcelas. Aunado a la clasificación de parcelas por ubicación, solo el 10% de los sitios de muestreo se localizaron en zonas internas, a diferencia del resto que se encuentran cercanos a algún tipo de desarrollo urbano. Lo que deja en duda si agentes externos (sobrepastoreo, recolección, cambios de uso de suelo, etc.) a su hábitat afectan o modifican la abundancia de la especie. A esto se puede agregar lo expuesto por Valenzuela et al. (2015) y Villanueva et al. (2016) donde aseveran las amenazas en zonas áridas y semiáridas del país, debido a sus condiciones medio ambientales extremas y los cambios de uso de suelo principalmente; donde además hacen énfasis en la fragilidad de la familia Cactaceae.

En la Tabla 2, se observa que ocho de los sitios de muestreo están cercanos a zona urbana, otros ocho contiguos a caminos o carreteras, dos colindantes a construcción de carreteras y dos en zonas internas. Esto indica que el 90% de los sitios estudiados se encuentran cercanos a algún tipo de desarrollo urbano; por lo que se puede considerar la vulnerabilidad de la especie de estudio. Tomando en cuenta el primer registro de la especie en 1908, reportado por Bravo-Hollis & Sánchez-Mejorada en 1991, el cual ubicó a la planta en lomeríos de la ciudad de Chihuahua; y su propio registro de 1991 especificó una distancia de 20 km de la ciudad pero sin dar una orientación. De 1991 a la fecha, la ciudad de Chihuahua aumentó su extensión territorial conforme al crecimiento poblacional que abarcó casi 1,000 ha en terreno (IMPLAN 2016). Observando el mapa de ubicación de los sitios en el presente estudio, muchos de los lomeríos mencionados en 1991 ya están urbanizados o muy cercanos a alguna área en desarrollo.

La vegetación encontrada corresponde a los dos tipos de vegetación MDM y MDR mencionados por Rzedowski (2006) y Lebgue & Quintana (2013); corroborando, así mismo, lo señalado por Lebgue & Quintana (2013) que *Coryphantha chihuahuensis* se desarrolla en los dos tipos de matorrales, aunque se haya observado una fuerte tendencia a MDM en este estudio. Además, las tres especies asociadas con mayor abundancia: *Aloysia wrightii* (Sp4), *Tecoma stans* (Sp18) y *Mimosa aculeatifolia* (Sp14), se encuentran en los dos matorrales. Por lo anterior, es probable que el habitat real de *C. chihuahuensis* sea MDM y los sitios detectados como MDR sean puntos de transición entre ambos tipos de matorral. Esto difiere con Lara-Juárez et al. (2016), los cuales mencionan que el tipo de vegetación predominante para cactáceas es MDR. Sin embargo, el estudio realizado por Alanis-Rodriguez et al. (2015) lo reafirma, ya que demostraron que en un mismo tipo de vegetación en zonas distintas, se encuentran asociaciones vegetales diferentes.

Estos registro de elevaciones de la especie (1220 y 1655 msnm) están dentro del rango (1200 y 1700 msnm) expuesto por Lebgue & Quintana (2013).

CONCLUSIONES
Coryphantha chihuahuensis tiene como rango de tolerancia biótico los matorrales desérticos, principalmente el Matorral Desértico Micrófilo y en menor proporción el Matorral Desértico Rosetófilo; se asocia con *Aloysia wrightii* y *Tecoma stans*, ambas especies se encuentran en forma

abundante en los dos tipos de vegetación. La presencia de estas especies asociadas y aunada a algunas condiciones físico-ambientales del hábitat, como laderas rocosas, son determinantes en la ubicación de *C. chihuahuensis*.

Como conclusión final se estima que *Coryphantha chihuahuensis* es una especie muy vulnerable, tanto por las atribuciones como por las amenazas propias de la familia. El conocimiento de la misma ayudaría a su protección y conservación, sobre todo entre las poblaciones aledañas a su hábitat. Por sus condiciones y características particulares *C. chihuahuensis* podría llegar a ser una especie emblemática con porte de identidad para la ciudad de Chihuahua. Sin embargo, se recomienda ampliar la investigación para formalizar su estatus, así como la difusión sobre la importancia de esta especie para el estado de Chihuahua.

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Tabla 1. Sitios de muestreo, punto central de cada parcela.

ID	Lugar	X	Y
1	Camino a Horcasitas	28° 25´08"	105° 49´18"
2	Cerca Bachiniva	28° 23´59"	105° 43´47"
3	Grutas Nombre de Dios	28° 42´20"	106° 04´48"
4	Granjas universidad	28° 33´13"	106° 06´19"
5	Cerro San Sebastián	28° 42´18"	106° 09´41"
6	Libra Delicias- Juárez	28° 46´53"	106° 05´54"
7	Nombre de Dios feria Santa Rita	28° 39´10"	106° 02´55"
8	Presa las vírgenes	28° 09´18"	105° 37´30"
9	Carretera Delicias – Satevo	27° 59´08"	106° 05´15"
10	Delicias - Chih km. 201	28° 30´53"	105° 55´47"
11	Boulevard a Almada	28° 34´52"	106° 05´49"
12	Cerro grande	28° 35´12"	106° 02´57"
13	Municipio Aquiles Serdán	28° 34´14"	105° 50´04"
14	Ejido Labor de Terrazas	28° 32´21"	106° 09´24"
15	Prolongación Francisco Villa	28° 40´04"	106° 08´53"

16	Pista aviones prolongación Cantera	28° 38´57"	106° 11´02"
17	Cerro atrás CIMA	28° 37´24"	106° 08´10"
18	Carretera Aldama Autódromo	28° 49´21"	105° 57´34"
19	Carretera Aldama libramiento Juárez-Delicias	28° 45´24"	106° 02´16"
20	Centro Cerro Nombre de Dios	28° 42´57"	106° 04´06"

Tabla 2. Clasificación de parcelas por su ubicación.

Clasificación	No. Sitio de muestreo
Cercano a zona urbana	3, 4, 5, 7,8,12,15,17
Cercano a caminos, carreteras o brechas	1, 2, 10, 13, 14,16, 18,20
Cercano a carreteras en construcción	6,19
Zonas internas	9, 11

Tabla 3. Formas de vida encontradas en parcelas, número de especies, cantidad de registros y probabilidad de presencia.

Forma de vida	No. de especies por grupo	No. de registros	Especies con un registro (%)	Especies superior a 5 registros (%)	10 registros ó más (%)	Probabilidad Presencia (%)
Arbustivas	20	111	27.3	45	62.5	40.4
Herbáceas	22	56	36.4	15	12.5	20.4
Gramíneas	19	58	24.2	25	0	21.1
Cactáceas	10*	50**	12.1	152	25	18.2
TOTAL	71	275	46.5	28.2	11.1	

*9 sin *Coryphantha chihuahuensis* **30 sin *Coryphantha chihuahuensis*

Tabla 4. Arbustos. Clasificación de especies, registro y probabilidad de presencia.

Clave	Especie	Registros	Prob.1	Prob.3
Sp1	*Acacia angustissima*	2	10%	3%
Sp2	*Acacia constricta*	6	30%	10%
Sp3	*Acacia neovernicosa*	1	5%	1%
Sp4	*Aloysia wrightii*	19	95%	27%
Sp5	*Asclepias oenotheroides*	1	5%	1%
Sp6	*Baccharis*	1	5%	1%
Sp7	*Celtis pallida*	9	45%	13%
Sp8	*Condalia ericoides*	1	5%	1%
Sp9	*Dasylirion* sp.	2	10%	3%
Sp10	*Ephedra trifurca*	1	5%	1%
Sp11	*Fouquieria splendens*	7	35%	10%
Sp12	*Jatropha dioica*	10	50%	14%
Sp13	*Mimosa dysocarpa*	1	5%	1%
Sp14	*Mimosa aculeatifolia*	14	70%	20%
Sp15	*Nolina texana*	1	5%	1%
Sp16	*Prosopis glandulosa*	9	50%	13%
Sp17	*Senna wislizenii*	6	30%	9%
Sp18	*Tecoma stans*	18	90%	26%
Sp19	*Tiquilia greggii*	1	5%	1%
Sp20	*Ziziphus* sp.	1	5%	1%

Prob.1= Probabilidad de presencia por forma de vida; Prob.2= Probabilidad entre total de especies.

Tabla 5. Herbáceas. Clasificación de especies, registro y probabilidad de presencia.

Clave	Especie	Registros	Prob.1	Prob.2
H1	*Amoreuxia* sp.	1	5%	1%
H2	*Asclepias latifolia*	2	10%	3%
H3	*Aspicarpa humilis*	1	5%	1%
H4	*Bidens* sp.	1	5%	1%
H5	*Croton pottsii*	8	40%	11%
H6	*Cheilanthes villosa*	1	5%	1%
H7	*Chenopodium álbum*	1	5%	1%
H8	*Descurainia pinnata*	1	5%	1%
H9	*Datura stramonium*	1	5%	1%
H10	*Dichondra argéntea*	3	15%	4%
H11	*Evolvulus alsinoides*	7	35%	10%
H12	*Evolvulus sericeus*	2	10%	3%
H13	*Hoffmannseggia* sp.	1	5%	1%
H14	*Ipomoea* sp.	4	20%	6%
H15	*Oenothera triloba*	1	5%	1%
H16	*Portulaca pilosa*	2	10%	3%
H17	*Sida procumbens*	10	50%	14%
H18	*Solanum elaeagnifolium*	3	15%	4%
H19	*Sphaeralcea angustifolia*	3	15%	4%
H20	*Tidestromia lanuginosa*	1	5%	1%
H21	*Viguiera cordifolia*	1	5%	1%
H22	*Vicia* sp.	1	5%	1%

Prob. 1= Probabilidad de presencia por forma de vida; Prob.2= Probabilidad entre total de especies.

Tabla 6. Gramíneas. Clasificación de especies, registro y probabilidad de presencia.

Clave	Especie	Registros	Prob.1	Prob.2
Z1	*Aristida adscensionis*	6	30%	9%
Z2	*Aristida divaricata*	4	20%	6%
Z3	*Bouteloua curtipendula*	5	25%	7%
Z4	*Bouteloua gracilis*	2	10%	3%
Z5	*Bouteloua hirsuta*	1	5%	1%
Z6	*Buchloe dactyloides*	1	5%	1%
Z7	*Cenchrus ciliaris*	9	45%	13%
Z8	*Cynodon dactylon*	1	5%	1%
Z9	*Elyonurus barbiculmis*	1	5%	1%
Z10	*Eragrostis cilianensis*	1	5%	1%
Z11	*Heteropogon contortus*	8	40%	11%
Z12	*Leptoloma cognatum*	3	15%	4%
Z13	*Leptochloa dubia*	1	5%	1%
Z14	*Lycurus phleoides*	4	20%	6%
Z15	*Melinis repens*	5	25%	7%
Z16	*Panicum hallii*	1	5%	1%
Z17	*Pennisetum* sp.	1	5%	1%
Z18	*Setaria leucopila*	2	10%	3%
Z19	*Setaria macrostachya*	2	10%	3%

Prob. 1= Probabilidad de presencia por forma de vida; Prob.2= Probabilidad entre total de especies.

Tabla 7. Cactáceas. Clasificación de especies, registro y probabilidad de presencia.

Clave	Especie	Registros	Prob.1	Prob.2
C1	*Coryphantha delaetiana*	1	5%	1%
C2	*Coryphantha ramillosa*	3	15%	4%
C3	*Coryphantha robustispina*	1	5%	1%
C4	*Coryphantha sneedii*	1	5%	1%
C5	*Coryphantha tuberculosa*	1	5%	1%
C6	*Echinocereus enneacanthus*	3	15%	4%
C7	*Echinocereus pectinatus*	6	30%	9%
C8	*Opuntia* sp.	11	55%	16%
C9	*Opuntia imbricata*	3	15%	4%

Prob. 1= Probabilidad de presencia por forma de vida; Prob.2= Probabilidad entre total de especies.

Tabla 8. Población de *Coryphantha chihuahuensis* por sitio y su estima poblacional.

Sitio	Población	Estima poblacional
1	4	Baja
2	19	Alta
3	4	Baja
4	1	Baja
5	4	Baja
6	1	Baja
7	7	Media
8	23	Alta
9	2	Baja
10	3	Baja
11	7	Media
12	1	Baja
13	1	Baja
14	1	Baja
15	2	Baja
16	4	Baja
17	5	Media
18	2	Baja
19	11	Alta
20	7	Media

REASSESSMENT OF VARIATION
WITHIN *POLYGALA CRUCIATA* SENSU LATO (POLYGALACEAE)

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ABSTRACT
Herbarium research confirms the presence of two distinct entities within *Polygala cruciata* sensu lato, each of which we treat as species. *Polygala cruciata* is nearly endemic to the Coastal Plain, with local disjunctions inland, whereas *P. aquilonia* is northern with populations southward in the Appalachian Mountains and southward along the coast to Virginia.

Several eastern North American floras have distinguished two intraspecific entities within *Polygala cruciata* L. Fernald (1950) and Weakley (2015) have recognized these as varieties –– *P. cruciata* var. *cruciata* and var. *aquilonia* Fernald & Schubert. A few other floras (e.g., Mohlenbrock 2014), in the range of only one of the varieties, specify that variety but do not provide a rationale. Haines (2011) treated two entities at subspecific rank (a *nom. illeg.* because of failure to cite the basionym publication). The characters used by Fernald & Schubert (1948) are leaf width, width of the inflorescence, and length of the peduncle. These treatments appear to rely strictly on Fernald & Schubert (1948), with no evidence of new and independent assessments of the characters used in the original segregation of var. *aquilonia* or of the introduction of new characters — Fernald (1950) and Weakley (2015) essentially repeated the characters from Fernald & Schubert (1948), while Haines (2010, 2011) mentioned the same characters generally ["the northern taxon (*aquilonia*) has broader leaf blades, shorter peduncles, and narrower racemes compared with the southern taxon (*cruciata*)"] and asserted that "recognition of these taxa as geographic subspecies is appropriate." Other floras covering portions of the distribution of *P. cruciata* (Gleason 1952; Gleason & Cronquist 1990; Weakley, Ludwig, & Townsend 2012; Tennessee Flora Committee 2015) do not recognize two taxonomic entities but are tacit in their reasoning, not providing a rationale or evidence.

Weakley's Flora of the Southern and Mid-Atlantic States (2015) has recognized *Polygala cruciata* var. *cruciata* and *P. cruciata* var. *aquilonia*. In general terms, var. *cruciata* has been considered to be southern in distribution and occurs mostly on the Coastal Plain, whereas var. *aquilonia* is northern and occurs inland as well as coastally. As noted by Fernald and Schubert (1948), there appears to be a zone of overlap in eastern Virginia. A taxonomic assessment seems long overdue (nearly 70 years after their initial recognition): should two taxa be recognized (and at what taxonomic rank), by what characters might they be recognized, and what are their detailed distributions (including areas of overlap)?

METHODS
We reviewed all specimens at NCU, ODU, VPI, and WILLI, concentrating our research in the area of geographical overlap of the two varieties. Bill McAvoy examined specimens from Delaware at DOV and PH and Wes Knapp provided records from Maryland. Other distribution records came from state floras and vascular plant atlases. We assessed the morphological characters used by Weakley (2015) in order to find those most effective.
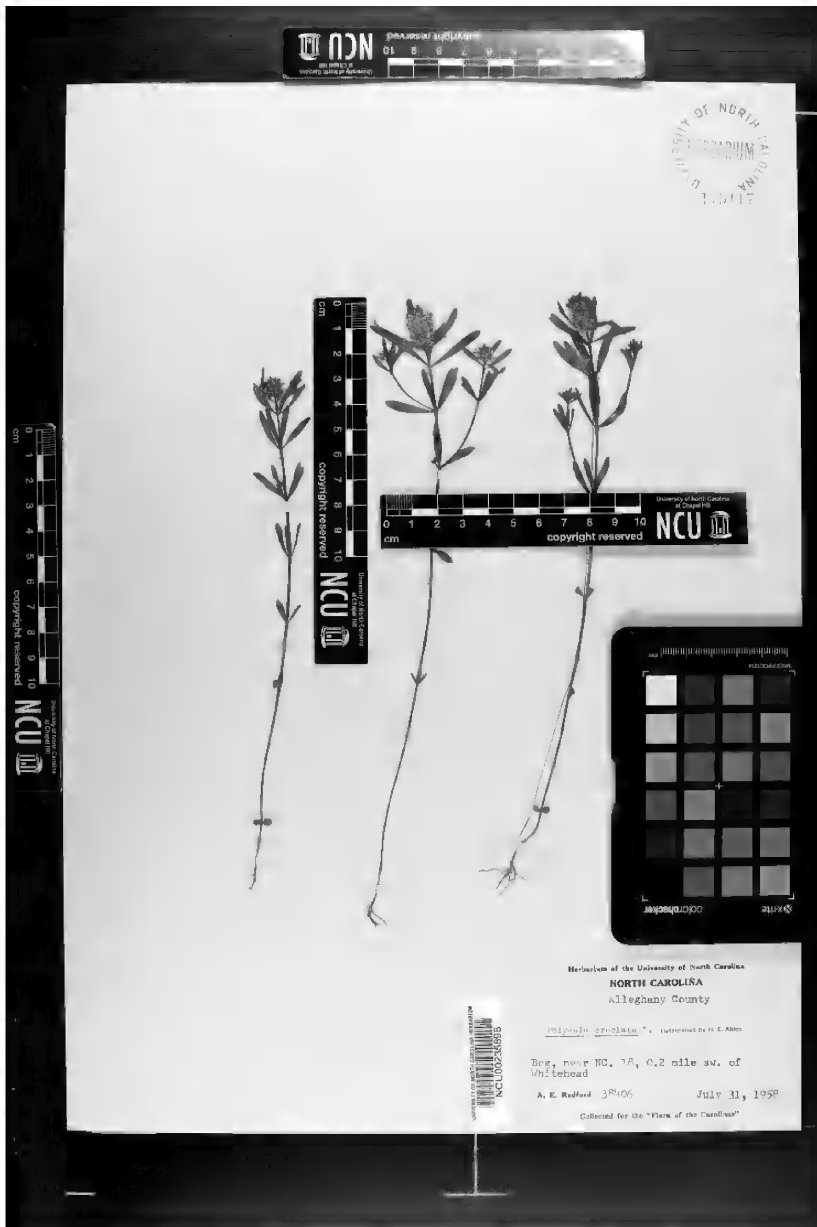
Figure 1. Specimen of *Polygala aquilonia* from the southern Appalachian Mountains. Note short floral axis.

Figure 2. Specimen of *Polygala cruciata* from the Coastal Plain of North Carolina. Note elongate floral axis.

Figure 3. *Polygala cruciata,* not fully developed, from the Coastal Plain of North Carolina. Note short floral axis.

Leaf width. Measurements of 23 leaves from as many specimens yielded a mean width of 2.1 mm for var. *cruciata*, with a range of 1.0-3.5 (-5) mm; a mean width of 2.9 mm for var. *aquilonia*, with a range of 1.5-4.5 mm. While a somewhat useful character, leaf width overlaps considerably and we excluded it from our key.

Raceme width. Measurements of 22 racemes yielded a mean for var. *cruciata* of 12.0 mm, with a range 10-15 mm; a mean for var. *aquilonia* of 9.9 mm, with a range of 8.5-12 mm. Contrary to Weakley's key, we found that no racemes of var. *cruciata* exceeded 15 mm; at least there are none on specimens at the herbaria searched. Visually, racemes of the more southern specimens certainly appeared to be broader than northern specimens.

Corolla wing length. Fernald and Schubert (1948) stated that the corolla wings of var. *cruciata* are longer than broad, 3.5-5.5 mm long, while in var. *aquilonia* wings are about as wide as long, 2.5-4 mm long. Measurements of 24 wings (without subulate tips) yielded a mean length for var. *cruciata* of 3.7 mm, with a range of 3.1-4.2 mm; a mean length for var. *aquilonia* of 3.3 mm, with a range of 3.0-3.7 mm.

Peduncle length. We assumed that "peduncle" meant the distance from the uppermost leaf to the first flower or flower bract, this being the customary use of the term. This may be the wrong interpretation, for Weakley (2015), Fernald and Schubert (1948), and Haines (2010, 2011) did not define the term as they used it in *Polygala cruciata*. They give peduncle lengths up to 40 mm for var. *cruciata*, whereas we measured none greater than 9 mm. We then re-measured peduncles to include the entire <u>floral axis</u> from the uppermost leaf to the tip of the inflorescence (20 specimens each variety). Thus measured, "peduncle" length ranged from 10-23 mm for var. *aquilonia*, with a mean of 16 mm (Fig. 1). For var. *cruciata*, "peduncle" length ranged from 11-96 mm (Fig. 2). In specimens solely from the state of North Carolina, the range was 11-64 mm, with a mean of 35 mm. It seems clear that southern and Coastal Plain plants develop long "peduncles" due to the continued growth of the inflorescence. This produces a markedly long axis that bears many persistent bracts along its length as corollas fall off. Based on specimens examined, inflorescences of northern and inland plants do not continue to elongate (or very little), and therefore appear to be sessile or subsessile. In this paper we use the term "floral axis" to describe the combined peduncle and inflorescence rachis. Note: specimens of var. *cruciata* collected early in the flowering period (Fig. 3) will show minimal elongation of the floral axis and thus mimic var. *aquilonia* in that character; however, raceme width will point towards var. *cruciata*.

RESULTS
By using a combination of raceme width and peduncle length, we were able to effectively distinguish two taxa; see the following key. Note: early in its flowering period var. *cruciata* will show minimal elongation of the floral axis and plants may key to var. *aquilonia*. Be sure to also measure raceme width as supporting evidence.

1. Floral axis length 11–64 (–96) mm, mean 35; raceme width 10–15 mm, mean 12; corolla wing length mean 3.7 mm ....**Polygala cruciata**
1. Floral axis length 10–23 mm, mean 16; raceme width 8.5–11 (–12) mm, mean 9.9; corolla wing length mean 3.3 mm ....**Polygala aquilonia**

TAXONOMIC TREATMENT
Polygala cruciata L., Sp. Pl., 706. 1753. **TYPE: Virginia**, without locality, *J. Clayton 157* (lectotype BM), designated by Reveal in Jarvis (2007, p. 755). Fernald & Schubert (1948) made a reasoned argument that *Clayton 157* represents the southern entity and not the northern, and we concur.

Polygala aquilonia (Fern. & B.G. Schub.) Sorrie & Weakley, **comb. et stat. nov.** *Polygala cruciata* var. *aquilonia* Fern. & B.G. Schub., Rhodora 50: 163, pl. 1100. 1948. TYPE: **Connecticut**. [Fairfield Co.]: Stratford, inner edge of salt-marsh, 30 Aug 1896, *E.H. Eames s.n.* (holotype: GH).

Polygala cruciata subsp. *aquilonia* (Fern. & B.G. Schub.) A. Haines [nom. illeg., without citation of basionym publication], Stantec Bot. Notes 13: 5. 2010.

Our reasoning is based on the following points. (1) The vast majority of specimens are clearly separated morphologically, using the characters in our key. We had little trouble in assigning specimens to one or the other species, which indicates that the characters are consistent. While equivocal specimens occur, they represent a small percentage of the hundreds of sheets we examined from throughout the ranges of the two species. A list of equivocal specimens is included in the following section. (2) The ranges of the two species are largely allopatric, with relatively small areas of overlap (Fig. 4 and Fig. 5, below). (3) Within the two overlap zones the species maintain their morphological distinction, with the exception of a small number of "intermediates." Based on existing evidence, we conclude that these two entities are separate evolutionary lineages at this time, satisfying criteria for species rank under modern species concepts, including the evolutionary species concept and de Queiroz's (1998, 2007) general lineage species concept.

Examples of equivocal specimens
(1) Clay Co., North Carolina (*Radford & Duke 6436,* NCU). Racemes are 12 mm wide, leaves 4.0-4.5 mm wide. The peduncles vary from 18-35 mm long and with few or no exposed bracts.
(2) Montgomery Co., Kentucky (*Wharton 408*, NCU). Racemes are 8-10 mm wide, peduncles 17-35 mm long, leaves 2-5 mm wide. Flower bracts are numerous on one plant, absent on another.
(3) Fentress Co., Tennessee (*Rock 987*, NCU). Leaves <3 mm wide, racemes 10-12 mm wide, peduncles vary from 18-22 mm long. Some flower bracts are exposed.
(4) Lincoln Co., Tennessee (*Sharp et al. 4876*, VPI). Racemes measure up to 12 mm wide, peduncles up to 28 mm long.
(5) Polk Co., Tennessee (*Rogers 31402*, NCU). Racemes are up to 14 mm wide but sessile.
(6) Brunswick County, Virginia (*Mikula 3467*, WILLI). Racemes are up to 12 mm wide but peduncles up to 22 mm long.
(7) In addition, Bill McAvoy (pers. comm.) has measured several equivocal specimens from Delaware.

Other taxonomic considerations
The Coastal Plain of the Delmarva Peninsula and southeastern Virginia constitutes the primary overlap area for the two species, although the extent of the overlap zone has only now been worked out in detail. Fernald and Schubert (1948) stated that "...in eastern Virginia typical *Polygala cruciata* and var. *aquilonia* obviously merge..." The online atlas of Virginia plants (Digital Atlas 2016) does not distinguish between taxa. The online atlas of Maryland plants (Maryland 2016) lists only var. *cruciata* for the state (Wicomico Co.); however, the photo accompanying the text shows sessile racemes and relatively broad leaves, suggestive of *P. aquilonia*. In Delaware, McAvoy and Bennett (2001) included only var. *aquilonia*. As a result of our research, we now know that both species occur in eastern Virginia, Maryland, and Delaware. Moreover, we extend the area of overlap to southern New Jersey, with a specimen of *P. cruciata* from Cumberland Co.: 1 mi NW of Bennetts Mill, clay-bottomed pond-hole, 25 Sep 1938, *Long 53141* (VPI). On this specimen, the raceme width is 15 mm and the floral axis is 31 mm.

A secondary area of overlap is in the Eastern Highland Rim and Cumberland Plateau of central Tennessee (Fentress Co. south to Coffee and Grundy counties). This region also includes

plants of equivocal identity (examples listed above) in close proximity to typical plants, which maintain clear identity.

Haines (2010) suggested that the two taxa occupy somewhat different habitat types, based on Fernald and Schubert (1948), who stated that "... the generally more northern or inland var. *aquilonia* is a plant of usually less saturatedly wet habitats and from Delaware northward it is partial to the outer coastal or coastwise region, even the upper borders of salt-marshes." As examples of "saturatedly wet," Fernald and Schubert cited "wet pineland," "low pineland," "boggy savannas," "swamps," and "pine-barren swamps." While we agree that there appears to be a shift from seasonally saturated habitats northward to more or less permanently saturated habitats southward, we wish to clear up some misinterpretations regarding older specimen label data. For decades we have studied plant communities of the Southeast and assessed specimen label data from collectors such as Curtiss, Chapman, Harper, and Tracy. In the 1800s and early 1900s collectors routinely wrote "swamp" or "bog" not to mean a permanently wet to inundated forest or a peat bog in the sense of northern botanists but to cover a diverse array of permanently to seasonally saturated, fire-prone habitats. Critical to the southern habitats is seepage from adjacent low slopes, or a permanently high water table, but no standing water as "swamp" would suggest, nor accumulation of peat as "bog" would suggest. Graminoids and low shrubs dominate beneath a canopy of moderately dense to very sparse pines, the whole kept free of dense shrubs and saplings by recurring fires.

Range of *Polygala cruciata* (Figure 4)
Coastal Plain from southern New Jersey to southern Florida, eastern Texas, southeastern Oklahoma, and central Arkansas It is a rare disjunct in Bartow Co., Georgia (sinkhole pond), Greenville Co., South Carolina (montane seepage bog), Coffee and Bledsoe counties, Tennessee (Manchester Prairie, etc.) –– all areas known for Coastal Plain disjuncts. Fernald and Schubert (1948) also cited specimens from Grundy and Van Buren counties, Tennessee (GH); Gentry et al. (2013) have mapped it disjunctly in Benton Co., Arkansas.
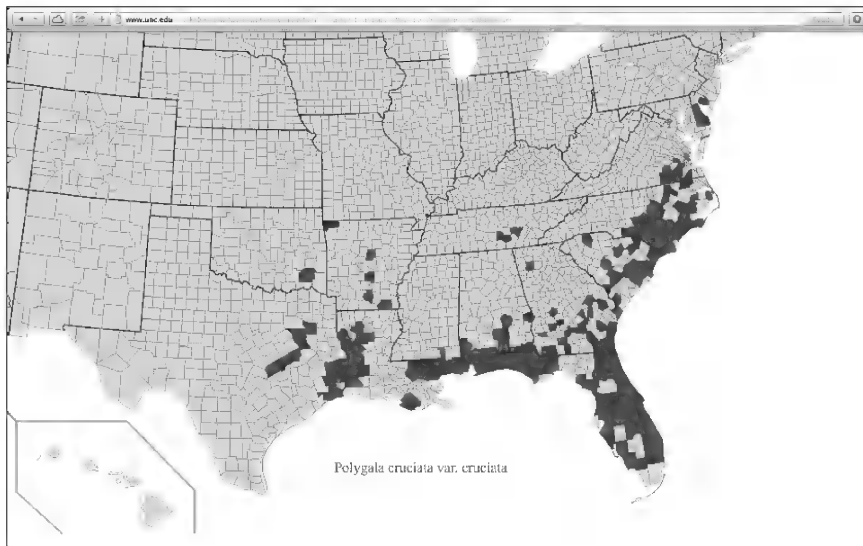
Figure 4. Range of *Polygala cruciata*.

A check of additional specimens from other herbaria will improve the range maps, and perhaps increase the number of disjunct localities. At the present, P. *cruciata* is treated as a Coastal Plain endemic with a few disjunctions.
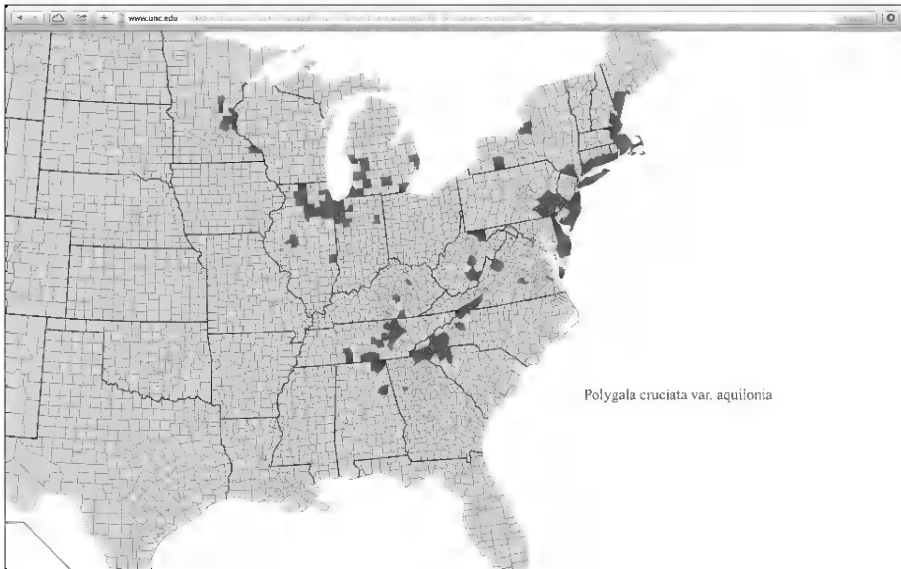
Figure 5. Range of *Polygala aquilonia*.

Range of *Polygala aquilonia* (Figure 5)

Southern Maine to southeastern Minnesota, south to southeastern Virginia, and upland regions of central Kentucky and Tennessee. Also Southern Applachian Mountains from Virginia and West Virginia to northeastern Alabama. The PLANTS database maps it in Ohio, Wisconsin, and Ontario, Canada. This variety occurs in coastal counties southward to Northampton County, Virginia. On the mainland of Virginia (excluding the mountains) *Polygala aquilonia* is apparently rare: York County (*Wright s.n.*, WILLI) and Powhatan County (*Wieboldt et al. 1161*, VPI).

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NEW COMBINATION IN *ASTRAGALUS* (FABACEAE)

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ABSTRACT

Recent molecular phylogenetic analyses have established that the four varieties of *Astragalus cusickii* are three distinct, monophyletic clades: *A. cusickii* var. *cusickii* and *A. cusickii* var. *flexilipes* form one clade, *A. cusickii* var. *sterilis* and *A. cusickii* var. *packardiae* each form the other two. Although relationships among the clades in the analyses are poorly resolved, they are also poorly resolved with respect to other recognized species in the genus. Morphological data provide unique synapomorphies for each of the clades and therefore we propose to recognize three distinct species, with *A. cusickii* var. *flexilipes* retained at the rank of variety. A new combination brings *A. cusickii* var. *packardiae* to species rank, as **Astragalus packardiae** (Barneby) J.F. Sm. & Zimmers, **comb. nov.**, whereas *A. sterilis* has already been published.

Astragalus L. is a diverse group of approximately 2500 species (Frodin 2004; Lock & Schrire 2005; Mabberley 2008) and has a rich diversity in four geographic areas (southwest and south-central Asia, the Sino-Himalayan region, the Mediterranean Basin, and western North America; in addition the Andes in South America have at least 100 species. Second to Eurasia in terms of species diversity is the New World, with approximately 400-450 species. The Intermountain Region of western North America (Barneby 1989) is especially diverse, and an estimated 70 species of *Astragalus* can be found in Idaho alone, including several endemic taxa (Mancuso 1999). The monophyly of *Astragalus* sensu stricto has been well-supported (Sanderson 1991; Sanderson & Doyle 1993; Wojciechowski et al. 1993, 1999), but many species-level relationships within the genus remain poorly resolved and most species in the Old World had not been revised since the late 19th century (Bunge 1868, 1869; Taubert 1894) until only recently (Podlech & Zarre 2013).

A recent phylogenetic analysis focusing on the four varieties of *Astragalus cusickii* A. Gray (1878) determined that the group could be divided into three monophyletic groups (Zimmers et al. 2017); *A. cusickii* var. *sterilis* (Barneby) Barneby (1989)*, A. cusickii* var. *packardiae* Barneby (1989), and *A. cusickii* var. *cusickii/A. cusickii* var. *flexilipes* Barneby (1956). Relationships among the three clades and other species of *Astragalus* were not strongly supported, and additional tests could not reject a single monophyletic *A. cusickii*. However, the same tests could not reject a single monophyletic clade that included all four varieties of *A. cusickii* as well as *A. whitneyi* A. Gray (1865), which has always been recognized as a distinct species from *A. cusickii*. Given that closely related species are likely to be monophyletic (Scherson et al. 2005; Zimmers et al. 2017), we elevate two of the varieties of *A. cusickii* to species rank, based on the unified species concept (a monophyletic group diagnosably distinct from close relatives; de Queiroz 2005). This concept has been selected because (1) monophyly can be assessed, (2) morphological differences are known and presumably are the result of inheritance from a common ancestor, and (3) few studies address the breeding system of these plants. Recent studies of species in *Astragalus* have also employed monophyly with diagnosable differences between populations as the criteria for recognizing species (Scherson et al. 2008; Riahi et al. 2011). Therefore, we recognize *A. cusickii* var. *packardiae* and *A. cusickii* var. *sterilis* at the rank of species and make the new combination for *A. packardiae* here.

Astragalus packardiae (Barneby) J.F. Sm. & Zimmers, **comb. nov.** *Astragalus cusickii* A. Gray var. *packardiae* Barneby, Intermtn. Fl., Fabales, 3B: 79. 1989. **TYPE: USA. Idaho.** Payette Co.: on a small tributary of Dry Creek, 18 May 1980, *J. Grimes & P.L. Packard 1583* (holotype NY; isotype CIC!).

Astragalus cusickii is a sparsely leafy, multi-stemmed, perennial forb found in western Idaho, eastern Oregon, and the extreme southeast corner of Washington. *Astragalus cusickii* var. *cusickii* has the widest geographic distribution of the four varieties. It is found in western Idaho, eastern Oregon, and southeast Washington, although with a concentration in the Hells Canyon area. *Astragalus cusickii* var. *flexilipes* appears to be only weakly differentiated from *A. cusickii* var. *cusickii* by subtle morphological differences: small, purplish flowers, and oblique, half-ellipsoid pods (Barneby 1989). The distribution of *A. sterilis* Barneby (1949) is limited to a small geographic area in southeastern Oregon and adjacent southwestern Idaho. This variety is distinguished by its smaller leaflets and bright red mottling on its pods. It is considered rare and of conservation concern in both Oregon and Idaho. *Astragalus packardiae* is distinguished by its relative paucity of leaves on the stems, particularly distally, its relatively small purplish flowers, and its small, narrow pods. It is considered one of the rarest plant taxa in Idaho, restricted to an approximately 10 square-mile area in Payette County, Idaho (Mancuso 1999). It has become a high priority conservation concern due to its limited geographic distribution, small population size, habitat decline, and vulnerability of its habitat to multiple, ongoing disturbances and threats (Mancuso 2016).

Astragalus sterilis was originally described at specific rank (Barneby 1949). It was only with the publication of *The Intermountain Flora* that Barneby (1989) moved *A. sterilis* to the rank of variety and described *A. cusickii* var. *packardiae*. In the discussion of the treatment for *A. cusickii,* Barneby acknowledged that recent collections had led him to change his view of *A. sterilis* as a distinct species defined by "its rhizomatous, subterranean caudex (resembling that of *A. ceramicus*) which gave rise to colonies of solitary or paired, short, and densely branched stems" to a distinct ecotype differentiated from typical *A. cusickii* only by "uniformly very short leaflets, and by the bright mottling of the pod, a syndrome too weak to support specific status." He also recognized that *A. cusickii* var. *flexilipes* was only weakly differentiated from the type variety and that *A. cusickii* var. *packardiae* was similar to *A. cusickii* var. *flexilipes* but was highly localized and differentiated by the loss of leaflets in the upper leaves and the narrowly and symmetrically ellipsoid fruit. Despite his views of the ranking of these taxa, Barneby (1989) clearly recognized morphological differences of both *A. sterilis* and *A. packardiae.*

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GALACTIA (FABACEAE) IN FLORIDA:
COMMENTS ON FRANCK'S RECENT STUDY

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ABSTRACT

Review of recent taxonomic suggestions by A.R. Franck for *Galactia* in Florida finds that (1) *G. fasciculata* and *G. floridana* are distinct species, (2) the type of *G. brachypoda* is not a hybrid between *G. erecta* and *G. mollis*, thus Franck's newly proposed *G. michauxii* becomes a synonym of *G. brachypoda*, and (3) Franck's description of a endemic species narrowly distributed in southern Florida as *G. austrofloridensis* sp. nov. is reasonable, but its distinction is weakly supported; I identified it earlier as *G. grisebachii*, primarily a Caribbean species.

For taxa of *Galactia* in Florida, Franck (2017) has essentially reprised my treatment of the genus (for the USA, Nesom 2015), diverging from its taxonomy in three instances: (1) treatment of *G. fasciculata* Vail as a synonym of *G. floridana* Torr. & Gray; (2) interpretation of the type of G. *brachypoda* Torr. & Gray as a hybrid between *G. erecta* (Walt.) Vail and *G. mollis* Michx., then description as a new species (*G. michauxii* Franck) the plants that I identified as *G. brachypoda*; and (3) description as a new species (*G. autrofloridensis* Franck) the plants that I identified as *G. grisebachii* Urb., the consequence of interpreting the latter as a Caribbean endemic. These taxonomic disparities are discussed below.

(1) *Galactia fasciculata* vs. *Galactia floridana*

My treatment separated these two entities by habit and vesture, the contrasts below drawn from the descriptions I provided. Further, the ecologies of the two are distinct and, while they are partially sympatric, their geographic ranges also are distinct (see Figs. 1 and 2, including ecological information in the legends).

1. Stems procumbent, creeping, rooting at nodes, sometimes climbing-sprawling but not twining, densely short-tomentose to hirsute-villous with spreading-erect, irregularly oriented hairs; leaflets adaxially glabrous .... **Galactia floridana**
1. Stems high-climbing, twining; loosely strigose with short, loosely appressed, retrorse hairs; leaflets adaxially sparsely strigose-sericeous with loosely appressed hairs .... **Galactia fasciculata**

I noted that (2015, p. 11) "*Galactia fasciculata* is distinguished by its strongly lignescent, twining and high-climbing stems with densely and loosely retrorse-strigose vesture, coriaceous leaves dark and glossy above, and relatively short inflorescences with large flowers. It has sometimes been identified as *G. floridana* but the latter is completely distinct from *G. fasciculata* in its procumbent habit, tomentose to hirsute-villous stems, persistently hairy adaxial leaf surfaces, elongate inflorescences with distally positioned flowers, and villous calyces."

Franck (p. 147) noted that "Because of their similarities, *Galactia fasciculata* is here tentatively treated as a synonym of *G. floridana*." He emphasized (a) similarities in stem and calyx vesture, (b) the inconsistent production of fasciculate inflorescences in *G. floridana* (originally distinguished, but not by me, as fasciculate), and (c) a tendency for stems to curve and twine in *G. floridana*. While infraspecific variation may exist in vesture, it does not alter my essential characterizations of the two entities. Stem vesture of the types of *G. fasciculata* (including *G.*

volubilis var. *baltzelliana*, a synonym) is regularly retrorsely oriented and not like that characteristic of *G. floridana*. Stems in *G. floridana* sometimes may become loosely twining distally (procumbent and rooting at the nodes proximally) and even climb over low shrubs, but they are not like the climbing stems of *G. fasciculata*. *Lakela 25304* (Hernando Co., USF, digital image!) and *Lakela 253779* (Hillsborough Co., USF, digital image!), cited by Franck as examples of 'twining' habit in *G. floridana*, indeed clearly are *G. floridana* –– but different from the climbing, coiling stems of *G. fasciculata*. I did not find a difference between the two in inflorescence morphology.

A field study probably will resolve the question but based on evidence at hand, I remain convinced that *Galactia fasciculata* is a species distinct from *G. floridana*.
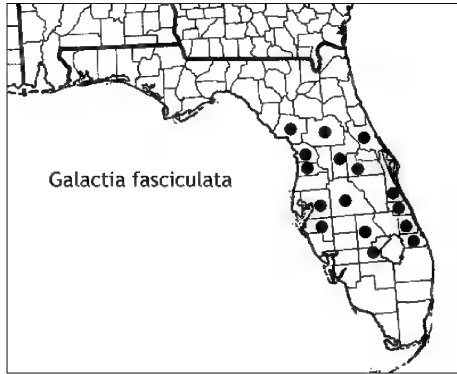
Figure 1. Distribution of *Galactia fasciculata*. Habitat: sand-pine scrub, dunes and hills with sand pine-oak, oak-hickory, scrubby flatwoods, river banks with live oak, longleaf pine, and saw palmetto, disturbed areas.
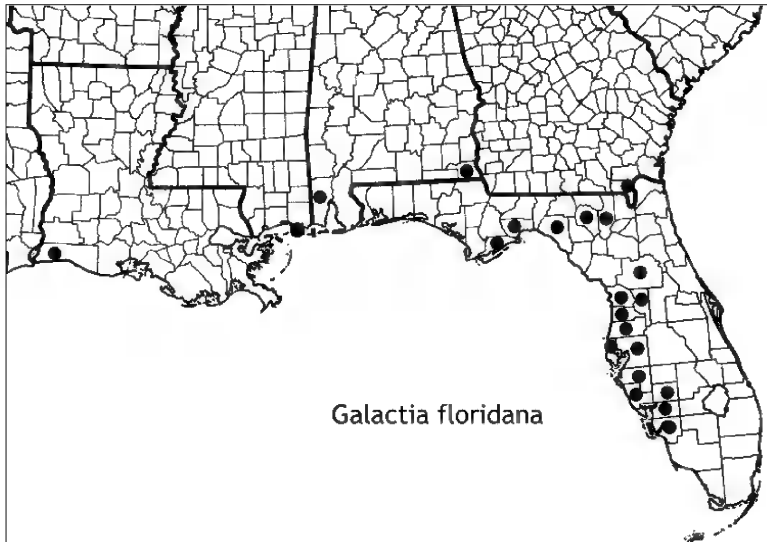
Figure 2. Distribution of *Galactia floridana*. Habitat: open pine woods, pine barrens, longleaf pine-turkey oak-blue oak woods, sandhill scrub, sandhills, roadsides.

Figure 3. Holotype of *Galactia brachypoda* Torr. & Gray. The habit is procumbent, vestiture short-strigose. Leaflets vary in shape from relatively narrow (as in the holotype) to more broadly elliptic.
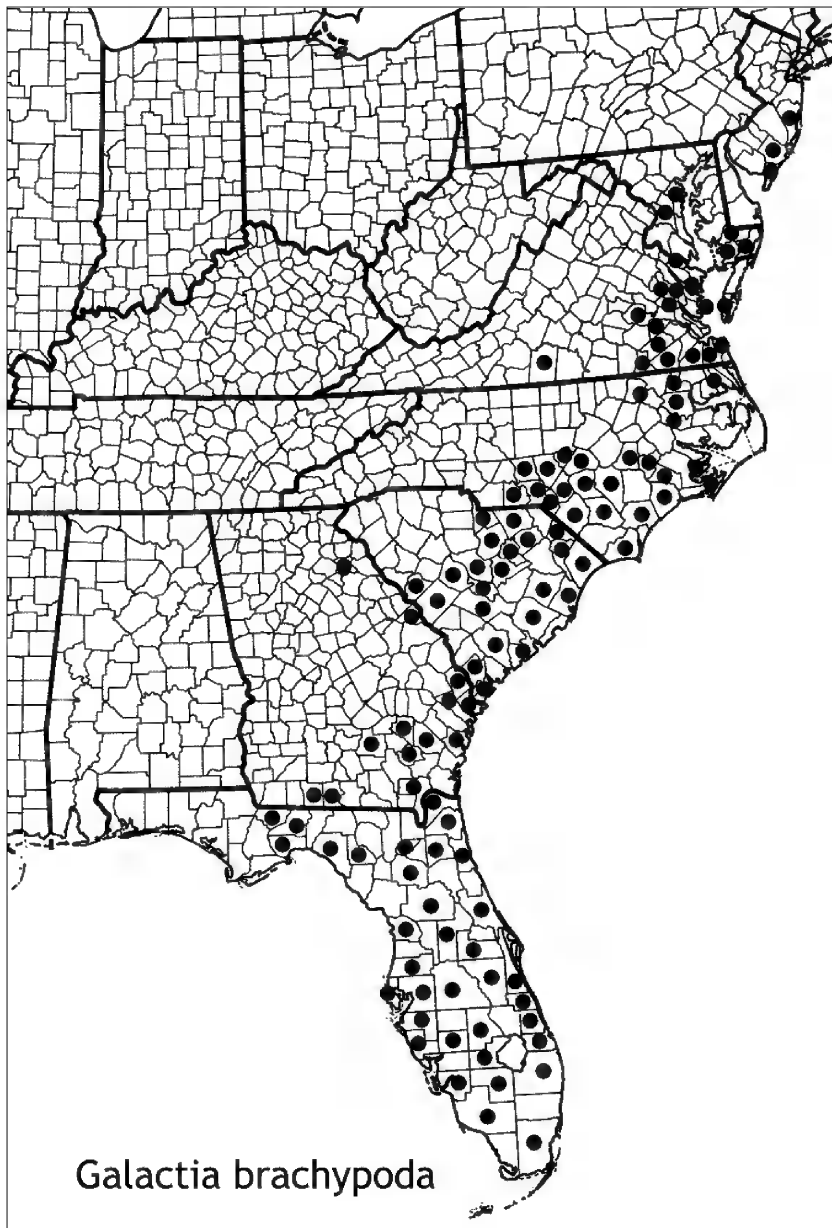
Figure 4. Distribution of *Galactia brachypoda*.

(2) The type of G. *brachypoda* and corresponding description of *G. michauxii* (sp. nov.)

Franck's rationale lies in his interpretation of the type specimen of G. *brachypoda* (Fig. 3; Figs. 6 and 7 of Franck). He sees it as a hybrid between *G. mollis* and *G. erecta*, noting as evidence "corollas drying or withering to a reddish color on specimens" (as in *G. mollis*) and "narrowly elliptic leaflets and petiole longer than the terminal leaflet" (as in *G. erecta*). He also points out difficulties of earlier botanists in distinguishing between *G. erecta* and *G. brachypoda* –– but these difficulties almost certainly reflect attempts to find two entities within a single species, i.e., within the species I identify as *G. erecta*. My earlier treatment provided a perspective (p. 12) on confusion in the typification of *G. brachypoda*.

> "Another Chapman collection at NY [besides the holotype/isotype] has been tentatively identified as *G. brachypoda* (8089) –– but it is *G. erecta*, which perhaps accounts for the placement of *G. brachypoda* in some accounts as a synonym of *G. erecta* (e.g., Vail described and keyed *G brachypoda* as having an erect habit). It also presumably accounts for why Isely (1998, p. 566) thought the type was so aberrant ("probably either a freak form of *G. erecta* or an exceptionally rare hybrid with one of the viny species") –– if not, the basis of his statement is not clear."

I see no clear evidence that the type of *Galactia brachypoda* is a *mollis-erecta* hybrid. Franck is hardly certain about the hypothesis –– he says "it seems likely that *G. erecta* and *G. mollis* hybridize" (p. 146) and notes that "*G. brachypoda* is possibly intermediate" between the two (p. 147). Instead, *G. brachypoda* appears to be representative of the species as I have identified it. The inflorescences of the holotype are immature and corolla color is ambiguous; the inflorescence axes (including peduncles) are 15–20 mm long (not like the sessile to subsessile inflorescences of *G. erecta*); stems are prostrate and up to 37 cm long, impossible to interpret as erect; vesture of the stems and calyces is very sparse and while the hair orientation cannot be seen, the plant apparently is part of the southern 'antrorse' population system of *G. brachypoda* (see Nesom 2015, p. 14). Leaf and leaflet morphology are variable in *G. brachypoda* (see comments in Nesom 2015) and the leaves of the holotype are easily within the bounds of variability of the species. Finally, Franck apparently had no difficulty in separating *G. brachypoda* of my interpretation (he treats it as a distinct species, with a different name) from *G. erecta*.

Franck found only three other collections that he thought might have a *mollis-erecta* hybrid origin (*Anderson 15642* from Baker Co., Ga.––FSU; *Duncan 17113* from Colquitt Co., Ga.––GA; *Chapman s.n.* from Gulf Co. Fla.––MO). An image of the Anderson collection is online — it indeed is closely similar to the type of *Galactia brachypoda*.

If accepted (as here) that *Galactia brachypoda* is correctly applied in my earlier treatment, then *G. michauxii* Franck is a synonym. In my concept the holotype of *G. michauxii* belongs among plants of the variable and broadly distributed *G. brachypoda*.

(3) Identification of *Galactia grisebachii* and description of *G. austrofloridensis* (as sp. nov.)

Numerous collections of a morphologically unambiguous species have been made from Dade, Lee, and Monroe counties in southern Florida (Fig. 6) –– from pinelands, pine-palmetto, hammocks, weedy grassland, sandy fields, and beaches. As characterized earlier (Nesom 2015, including Fig. 13, photos of the lectotype and isolectotype, here as Fig. 5), the stems are climbing-twining, filiform, sparsely and minutely strigose with antrorse hairs, leaves consistently linear-oblong, without raised veins, the inflorescence axis 10–40(–130) mm, and flowers solitary and axillary or 2–5(–10) in reduced pseudoracemes.

These plants had previously been recognized as *Galactia parvifolia* A. Rich. but I identified them as *G. grisebachii* Urb., establishing that *G. parvifolia* applies not to the Florida plants but instead to a species known from at least from Hispaniola, Cuba, and the Bahamas. *Galactia*
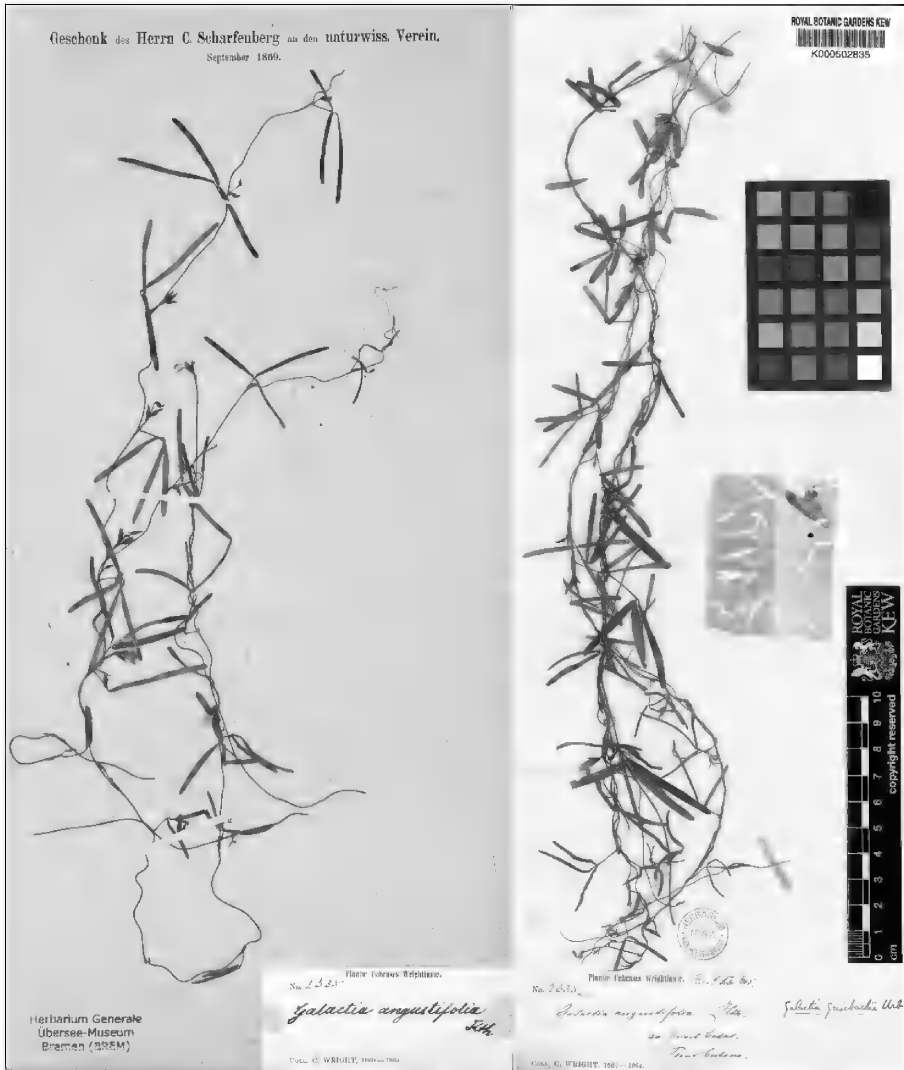
Figure 5. *Galactia grisebachii* Urb. Left. Lectotype, BREM   Right. Isolectotype, K.

parvifolia (2015, Fig. 14) has broadly oblong to oblong-elliptic leaflets from base to the top of the stem, distinct from the consistent linear shape of *G. grisebachii*. They are not the same species.

Franck observed that plants matching the lectotype of *Galactia grisebachii* (from Cuba) are restricted to the West Indies (at least Cuba, Jamaica, and Hispaniola), the Florida plants thus without

a name, which he then provided –– as *G. austrofloridensis* A.R. Franck. He contrasted *G. austrofloridensis* with *G. grisebachii* as follows: (a) long inflorescences often exserted beyond the leaves, with up to 9 flowers (vs. short inflorescences of *G. grisebachii* rarely exserted beyond the leaves, with up to 5 flowers) and (b) conspicuously raised-reticulate venation adaxially (vs. leaflets without raised-reticulate venation in *G. grisebachii*).
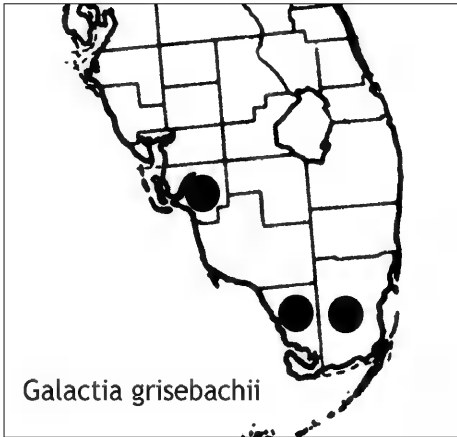
Figure 6. Distribution of *Galactia grisebachii* in Florida

In 2015, I considered the possibility that the Florida plants might be considered as an undescribed species but took the conservative route because of their morphological resemblance to *Galactia grisebachii* of the West Indies and because of their relatively common occurrence in ruderal habitats, which suggested they might not be native. Inflorescence axis length and number of flowers in the Florida plants is variable and overlaps with the West Indian plants. Whether a distinction in venation is constant remains to be clearly documented and affirmed.

In any case, Franck's hypothesis is reasonable, although he himself expressed doubt about it (p. 145): "Because of the obvious similarity and likely gradation between

Galactia austrofloridensis and *G. volubilis*, I find it unsatisfactory to recognize *G. austrofloridensis* at the species level and am wont to use infraspecific taxonomy, or lump it into *G. volubilis* as was done by Rogers (1949). However, many other taxa of the '*G. volubilis* group' could be recognized at the infraspecific level or synonymized for the same reasons. Until relationships are better understood within the '*G. volubilis* group,' *G. austrofloridensis* is reluctantly recognized."

I find no indication that *Galactia grisebachii* intergrades with *G. volubilis*, nor do I find credible Franck's assertion (p. 145) that *G. austrofloridensis* "has clear affinities with *G. volubilis*" (presumably he meant a close evolutionary/cladistic relationship), which I take to be no more than a guess. My own guess is that its relationships are closer to West Indian taxa if it is indeed not conspecific with one of them. Nor do I see the possibility that "many other taxa of the '*G. volubilis* group' could be recognized at the infraspecific level or synonymized."

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SOLIDAGO ALTISSIMA VAR. PLURICEPHLA (ASTERACEAE: ASTEREAE) IN AUSTRALIA, TONGA, AND HAWAII

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ABSTRACT

Herbarium collections of *Solidago* from Australia, Tonga, and Hawaii are reported here to be *Solidago altissima* L. var. *pluricephala* M.C. Johnston, which is previously unreported for these locations. Collections from K, MEL, and PERTH were included in a multivariate morphometric analysis comparing *S. altissima*, *S. canadensis*, *S. chilensis*, and *S. gigantea*. Also, a collection treated as *S. altissima* ssp. *altissima* from New Zealand was included in the analysis and confirmed to belong in the typical variety of the species. All specimens had densely hispid-strigose stems (sparsely to densely so proximally and densely so distally and in the inflorescence), lanceolate upper stem leaves with mostly entire margins and moderately to densely strigose abaxial main and prominent lateral veins. Specimens of var. *pluricephala* have secund conical inflorescences that are much longer than wide, while those of var. *altissima* tend to be nearly as wide as long.

Solidago altissima L. is native to North America and is a member of *S.* subsect. *Triplinerviae* (Torr. & A. Gray) Nesom (Semple & Cook 2006). The species includes plants with densely hispid-strigose stems (sparsely to densely so proximally and densely so distally and in the inflorescence), lanceolate upper stem leaves with mostly entire margins (lower and mid stem leaves are usually serrate) and moderately to densely strigose on the abaxial surface main and prominent lateral veins. Three varieties are recognized and differ in distribution, upper leaf shape, size and number of upper stem leaf serrations, and inflorescence shape (Semple et al. 2015). The typical race ssp./var. *altissima* is common to abundant in the northern half of the eastern deciduous forest region of North America. Variety *pluricephala* M.C. Johnston is native to the southeastern U.S. from Maryland to Florida west to Oklahoma and south Texas (Semple et al. 2015; not treated by Semple and Cook 2006 Flora North America). The subsp./var. *gilvocanescens* (Rydb.) Semple is native to the Great Plains prairies from Alberta to Manitoba south to northern Texas; it also occurs in scattered prairie habitats further east. Hexaploids of the species have been known to be invasive in south and eastern Asia and Oceania for many years though often reported as *S. canadensis* L. or under the synonym *S. canadensis* var. *scabra* (Muhl. ex Willd.) Torr. & Gray or as *S. altissima* (Li 1978; Iwatsuki 1995; Chen & Semple 2011, Sakata et al. 2015; Cheek and Semple 2016; Semple and Rao 2017; Australia's Virtual Herbarium 2017). The var. *altissima* was only recently confirmed to be adventive in Europe (Verloove et al. 2017); previous reports are likely for the diploid *S. canadensis* var. *hargeri* Fern. Only hexaploids of *S. altissima* have been reported from India (Sarkar et al. 1980; Bala and Gupta 2013; as *S. canadensis*), Japan (Huziwara, Y. 1962), and Taiwan (Peng & Hsu 1978). In North America, diploids and tetraploids occur in var. *gilvocanescens* with a few tetraploids and predominantly hexaploids being reported for var. *altissima* and var. *pluricephala* (Semple et al. 2015).

During a visit to Kew Herbarium (K; Thiers continuously updated) in late 2014, a number of Asian and Oceanian collections of what appeared to be either *S. chilensis* or *S. altissima* were examined among the general collections of *Solidago*. These were borrowed from K for more detailed

examination and scoring for comparison with specimens of the four species known to be invasives outside of North America: *S. altissima*, *S. candenisis*, *S. chilensis* (Lopez Laphitz and Semple 2015; Semple et al. 2017), and *S. gigantea* (Schlaepfer et al. 2008). Additional specimens of invasive *Solidago* were borrowed from MEL and PERTH to expand the sample of possible *S. altissima* plants from Australia and the second author provided data taken from greenhouse grown transplants of invasive species of *Solidago* from Australia to complete the sampling. The results of these new multivariate morphometric analyses and details on the specimens are present below.

MATERIALS AND METHODS

Herbarium specimens from BM, GH, F, K, LL, LP, MADS, MEL, MO, the J.K. Morton personal herbarium now deposited in TRT, MIN, NCU, NY, PERTH, TEX, USF, and WAT in MT were used in the multivariate analyses. A list of 14 vegetative and 16 floral traits scored was included in Semple et al. (2015) and is not repeated here. In total, 296 specimens of *S. altissima* (88 specimens included in Semple et al. 2015), *S. canadensis* (57 included in Semple et al. 2015), *S. chilensis* (89 specimens mostly included in Lopez Laphitz and Semple 2015), and *S. gigantea* Ait. (40 specimens, nearly all from Canada and the USA) were included in the analyses including the following:

S. altissima var *altissima*: **NEW ZEALAND**. Canterbury: NE of Christchurch, Harewood, 30 March 1968, *Healy 68/104* (K; dupl. CHR 231047; Figs. 1-2).

S. altissima var. *pluricephala*: **AUSTRALIA**: Queensland: Queensland: N of Kin Kin, Neusavale Rd., 26 Mar 2000, *Bean 16167* (MEL); Moreton, Ipswich, Bundamba Creek, Bergin's Hill Rd, 2 Apr 1993, *P.I. Forster PIF13192* (K; Figs. 3-4). South Australia: along River Torrens, Adelaide, 19 May 2015, greenhouse-grown transplant *Uesugi SAUT* (data from live plant, no voucher). Western Australia: Perth Station, May 1968, *Anon. s.n.* (PERTH). THAILAND. Bangkok, commonly cultivated, 7 Jul 1920, *Kerr s.n.* (K). TONGA. Tongatapu Is., Maufanga, 20 Apr 1959, *Soakai 622* (K; Figs. 5-6). USA. Hawaii: Oahu, Nu'Uanu Valley, Dowsett Tract, 10 Oct 1936, *Fosberg 13294* (K; dupl. US; Figs. 7-8).

S. altissima aff. var. *pluricephala*: **AUSTRALIA**. South Australia: Bray, Ackron Rd., 17 May 2015, greenhouse grown transplant, *Uesugi SAUA* (data from live plant, no voucher; identification tentative).

S. canadensis: **AUSTRALIA**. South Australia: Robe Rd., Greenways, 17 May 2015, greenhouse-grown transplant, *Uesugi SAUR* (data from live plant, no voucher).

All analyses were performed using SYSTAT v.10 (SPSS 2000). Two analysis were run to confirm the identification of *Anon. s.n.* (PERTH), *Bean 16167* (MEL), *Forster PIF13192* (K), *Fosberg 13294* (K), *Kerr s.n.* (K), *Healy 68/104* (K), *Soakai 622* (K), *Uesugi SAUT*, *Uesugi SAUR* and *Uesugi SAUA*. The first STEPWISE discriminant analysis included specimens of *S. altissima*, *S. canadensis*, *S. chilensis*, and *S. gigantea*. The second STEPWISE discriminant analysis was performed on 100 specimens of *S. altissima* (33 specimens of var. *altissima*; 29 specimens of var. *gilvocanescens*, and 38 specimens of var. *pluricephala*).

RESULTS AND DISCUSSION

Because some specimens were incomplete and lacked lower and mid stem portions of the shoot, only upper stem leaf traits were included. Ray floret ovary/fruit body length at anthesis and ray floret pappus length at anthesis were also not included due to high correlations with the disc floret traits.

In the STEPWISE discriminant analysis including 296 specimens in four species level a priori groups (*Solidago altissima*, *S. canadensis*, *S. chilensis*, and *S. gigantea*), the following ten traits were selected as useful in separating the four a priori groups in the analysis and are presented in order of decreasing F-to-remove values: number of upper leaf margin serrations (30.59), disc corolla length (21.28), outer phyllary length (21.31), number of disc florets (18.04), upper leaf width (13.91), disc

Figure 1. *Solidago altissima* var. *altissima* from New Zealand, *Healy 60_104* (K)
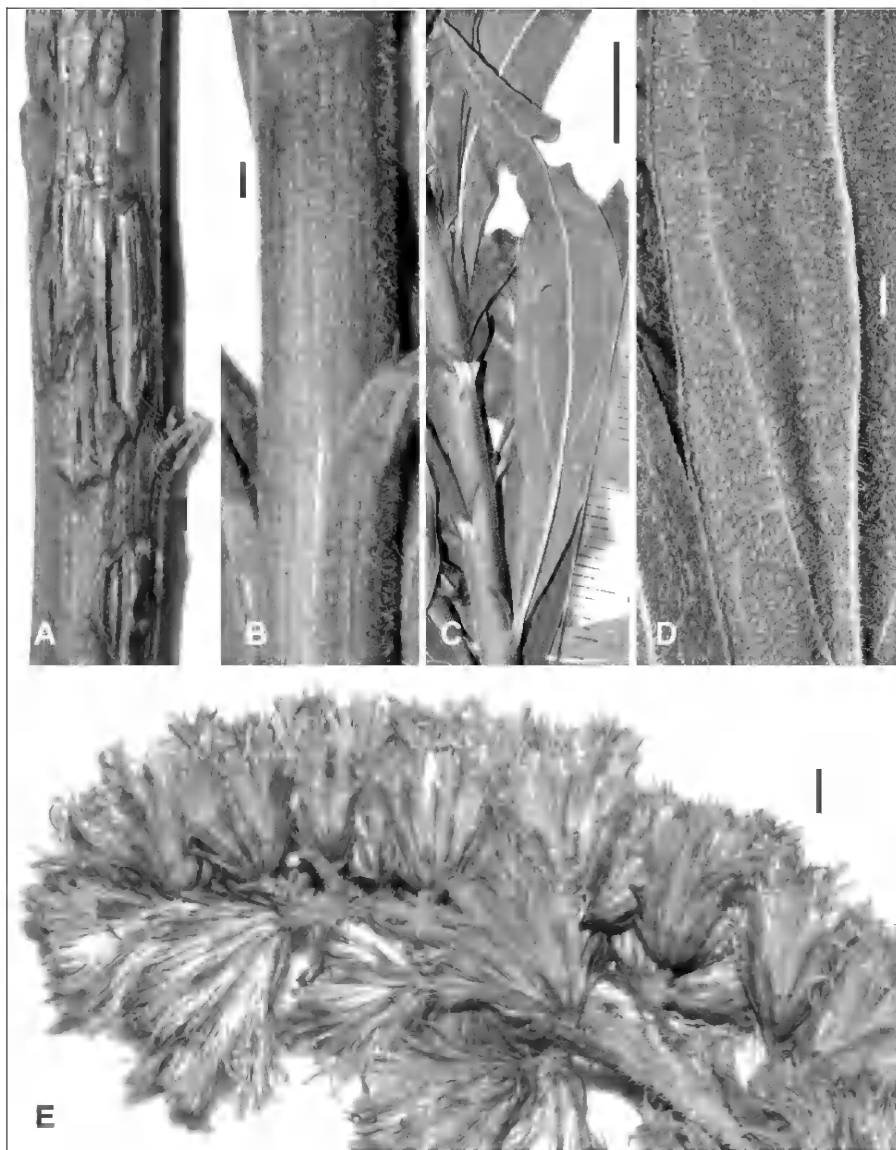
Figure 2. Details of *Solidago altissima* var. *altissima* from New Zealand, *Healy 60_104* (K). **A.** Lower stem. **B.** Mid stem. **C-D.** Upper mid stem leaf, abaxial surface. **E.** Heads. Scale bar = 1 mm in A, B, D and E; = 1 cm in C.
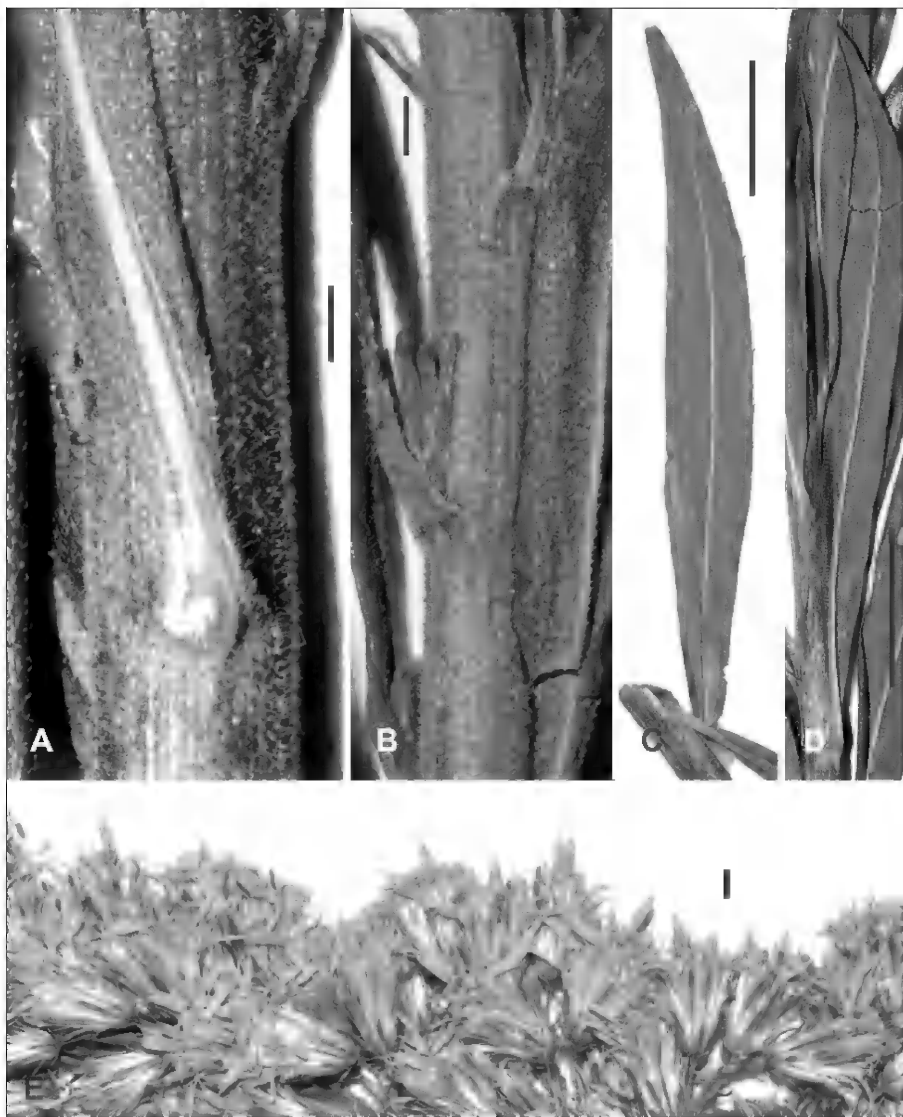
Figure 3. *Solidago altissima* var. *pluricephala* from eastern Australia, *Forster PIF13192* (K).

Figure 4. Details of *Solidago altissima* var. *pluricephala* from eastern Australia; *Forster PIF13291* (K). **A.** Mid stem. **B.** Upper stem. **C.** Mid stem leaf, abaxial surface. **D.** Upper stem leaf abaxial surface. **E.** Heads. Scale bars: = 1 mm in A, B and E; = 1 cm in C and D.

Figure 5. *Solidago altissima* var. *pluricephala* from Tonga, *Soakai 622* (K).
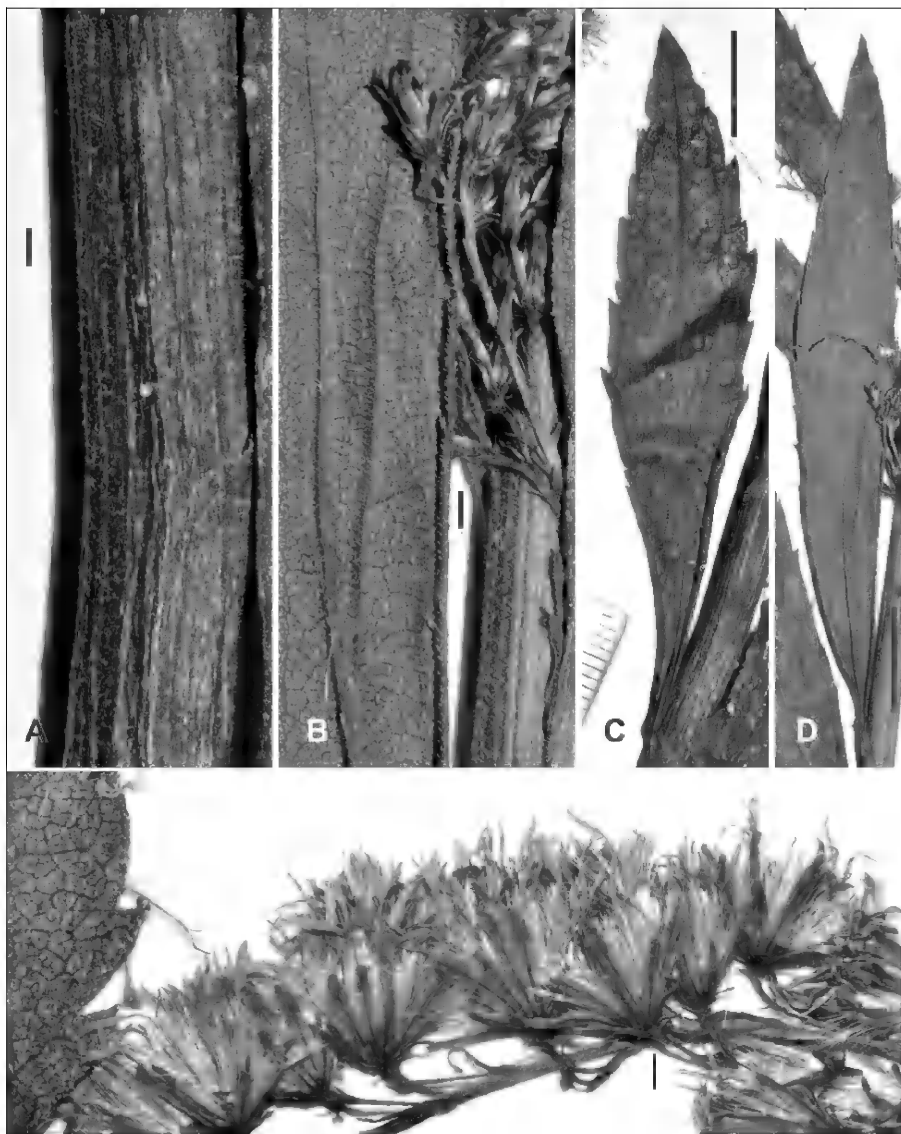
Figure 6. Details of *Solidago altissima* var. *pluricephala* from Tonga; *Soakai* 622 (K). **A.** Lower stem. **B.** Upper stem and leaf abaxial surface. **C.** Lower stem leaf, abaxial surface. **D.** Upper stem leaf, abaxial surface. **E.** Heads.   Scale bars: = 1 mm in A, B and E; = 1 cm in C and D.

Figure 7. *Solidago altissima* var. *pluricephala* from Hawaii; *Fosberg 13294* (K).
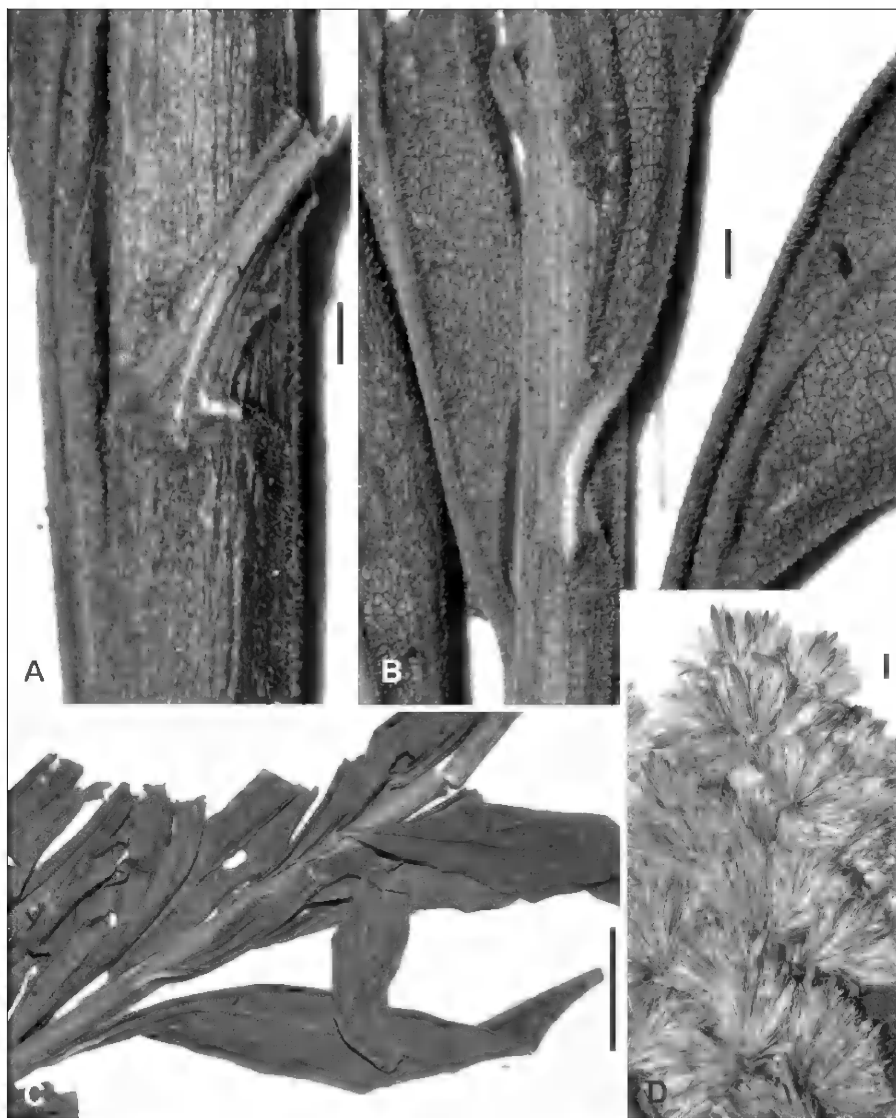
Figure 8. Details of *Solidago altissima* var. *pluricephala* from Hawaii; *Fosberg 13294* (K). **A.** Lower mid stem. **B.** Upper stem and abaxial leaf surfaces. **C.** Upper stem leaves. **D.** Heads. Scale bars: = 1 mm in A, B and D; = 1 cm in C.

Table 1. Between groups F-matrix for the four a priori groups analysis (df = 10   283).

Group	altissima	canadensis	chilensis
canadensis	31.180		
chilensis	74.882	86.564	
gigantea	38.706	33.039	57.985

Wilks' lambda = 0.0485 df = 10 3 292; Approx. F= 49.9922 df = 30 831   prob = 0.0000

corolla lobe length (11.24), upper leaf length (10.42), disc floret pappus length at anthesis (9.53), involucre height (9.98), and disc fruit body length at anthesis (8.95). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 1. F-values based on Mahalanobis distances between group centroids indicated the largest separation was between *S canadensis* and *S. chilensis* (86.564), and the least separation was between *S. altissima* and *S. canadensis* (31.180).

In the Classificatory Discriminant Analysis, correct assignments of specimens for taxa ranged from 89% to 99%. The Classification matrix and Jackknife classification matrix are presented in Table 2. One hundred of the 110 specimens of the *S. altissima* a priori group (91%) were assigned a posterior to *S. altissima*: *Kerr s.n.* (K) from Thailand with 100% probability, *Soakai 622* (K) from Tonga with 99% probability, *Fosberg 13294* (K) from Hawaii with 99% probability, *Bean 16167* (MEL) from Australia with 99% probability, *Forster PIF13192* (K) from Australia with 95% probability, *Healy 68/104* (K) from New Zealand with 90% probability, *Uesugi SAUT* from Australia with 90% probability, and *Anon. s.n.* (PERTH) from Australia with 86% probability. Fifty-one of the 57 specimens of the *S. canadensis* a priori group (89%) were assigned a posteriori to *S. canadensis*: *Uesugi SAUR* with 48% probability (46% to *S. altissima* and 5% to *S. gigantea*). Thirty-eight of the 40 specimens of the *S. gigantea* a priori group (95%) were assigned a posteriori to *S. gigantea*. The greenhouse-grown *Uesugi SAUA* was assigned to *S. gigantea* with 99% probability and tentatively treated in that a priori group in the analyses. However, discussion about its assignment to *S. gigantea* resulted in reassigning it tentatively to *S. altissima* var. *pluriacephala* based on greenhouse observations. Australia's Virtual Herbarium (2017) lists no collections of *S. gigantea* from Australia. Additional details of the results are not presented here.

Table 2. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of four a priori groups; a posteriori placements to groups in rows.

Group	altissima	canadensis	chilensis	gigantea	% correct
altissima	100	7	1	2	91
canadensis	3	51	0	3	89
chilensis	1	0	88	0	99
gigantea	0	1	1	38	95
Totals	104	59	90	43	94

Jackknifed classification matrix

Group	altissima	canadensis	chilensis	gigantea	% correct
altissima	100	7	1	2	91
canadensis	6	48	0	3	84
chilensis	1	1	86	1	97
gigantea	1	1	3	35	88
Totals	108	57	90	41	91

Two dimensional plots of CAN1 versus CAN3 and CAN1 versus CAN2 canonical scores for 296 specimens of *Solidago altissima*, *S. canadensis*, *S. chilensis*, and *S. gigantea* are presented in Fig. 9. Eigenvalues on the first three axes were 3.625, 1.369 and 0.883.
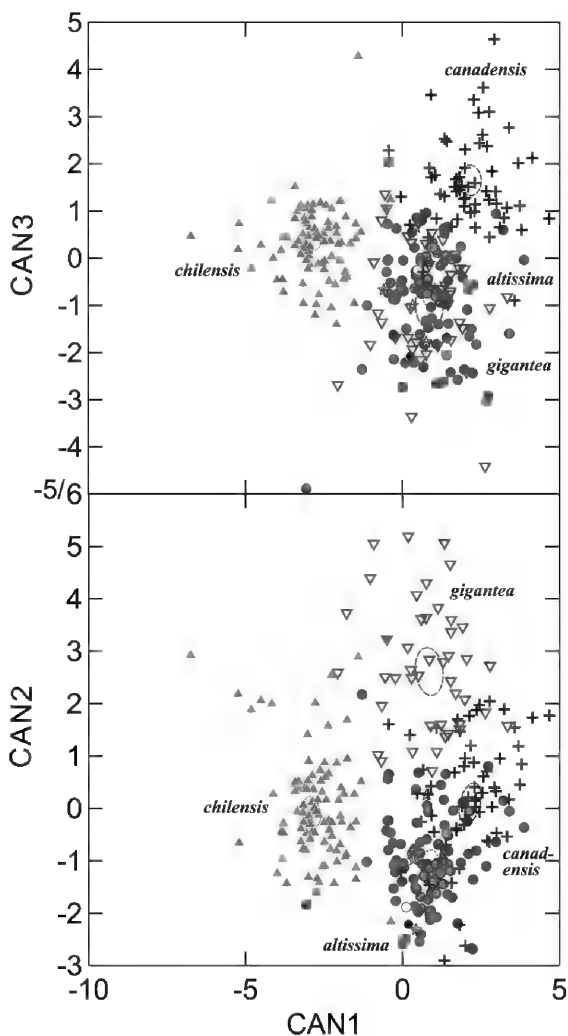
Figure 9. Plot of canonical scores (CAN1 vs CAN3 and CAN1 vs CAN2) for 296 specimens of adventive species of Solidago: *S. altissima* (red dots; from Australia - yellow stars; from New Zealand - yellow dot; from Tonga - orange dot; from Hawaii - white filled red circle; from Thailand - black dot), *S. canadensis* (black +s), *S. chilensis* (blue triangles), and *S. gigantea* (green inverted open triangles; from Australia - yellow filled green inverted triangle).

In the STEPWISE discriminant analysis of 100 specimens of three variety level a priori groups of *S. altissima* (var. *altissima*, var. *gilvocanescens* and var. *pluricephala*), the following seven traits were selected as best separating the groups and are listed in order of decreasing F-to-remove values: involucre height (30.96), disc corolla lobe length (9.05), number of disc florets (8.18), inner phyllary length (6.90), number of ray florets (5.99), outer phyllary length (4.99), and ray floret lamina width (4.21). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 3. F-values based on Mahalanobis distances between group centroids indicated the largest separation was between var. *gilvocanescens* and var. *pluricephala* (17.151), and the least separation was between var. *altissima* and var. *pluricephala* (5.181).

Table 3. Between groups F-matrix for the three a priori groups analysis (df = 7 91).

Group	altissima	gilvocanescens
gilvocanescens	12.241	
pluricephala	5.181	17.151

Wilks' lambda = 0.3077 df = 7 2 97; Approx. F= 10.4372 df = 14 182 prob = 0.0000

In the Classificatory Discriminant Analysis of the three varietal level a priori groups (var. *altissima*, var. *gilvocanescens* and var. *pluricephala*), percents of correct a posterori assignment to the same a priori group were 93% for var. *gilvocanescens*, 76% for var. *pluricephala*, and 61% for var. *altissima*. The Classification matrix and Jackknife classification matrix are presented in Table 4. *Healy 68/104* (K) in the var. *altissima* a priori group was assigned a posteriori to var. *altissima* with 70% probability (29% to var. *pluricephala* and 1% to var. *gilvocanescens*). *Uesugi SAUT* (Australia) in the var. *altissima* a priori group was assigned a posteriori to var. *altissima* with 63% probability (31% to var. *pluricephala* and 6% to var. *gilvocanescens*). The following collections in the var. *pluricephala* a priori group were assigned to var. *pluricephala*: *Bean 16167* (MEL; Queensland, Australia) with 98% probability, *Fosberg 13294* (K; Hawaii) with 97% probability, *Kerr s.n.* (K; Thailand) with 96% probability, *Anon. s.n.* (PERTH; Western Australia, Australia) with 96% probability, *Soakai 622* (K; Tonga) with 94% probability, and *Forster PIF13192* (K; Queensland, Australia) 93% probability. Further details of the results are not presented.

Table 4. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of three varietal level a priori groups; a posteriori placements to groups in rows.

Group	altissima	gilvocanescens	pluricephala	% correct
altissima	16	5	12	48
gilvocanescens	3	26	0	90
pluricephala	9	2	27	71
Totals	28	33	39	69

Jackknifed classification matrix

Group	altissima	gilvocanescens	pluricephala	% correct
altissima	20	5	8	61
gilvocanescens	2	27	0	93
pluricephala	8	1	29	76
Totals	30	33	37	76

A two dimensional plot of CAN1 versus CAN2 canonical scores for 100 specimens of *S. altissima* var. *altissima*, *S. altissima* var. *gilvocanescens* and *S. altissima* var. *pluricephala* is presented in Fig. 10. Eigenvalues on the first two axes were 1.392 and 0.359.
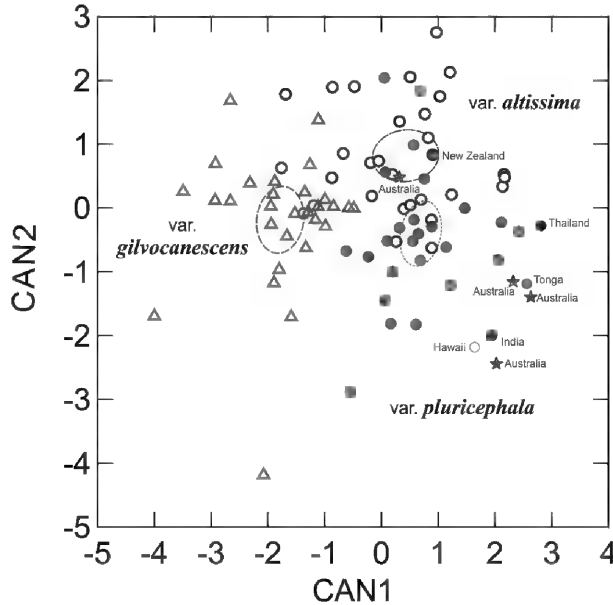
Figure 10. Plot of canonical scores (CAN1 vs CAN2) for 100 specimens of *Solidago altissima*: var. *altissima* (black circles; from New Zealand–yellow filled black circle), var. *gilvocanescens* (open blue triangles), and var. *pluricephala* (red dots; from Australia–yellow stars; from Tonga–orange dot; from Hawaii–white filled red circle; from Thailand–black dot; from India–green dot).

The results clearly show that *Solidago altissima* var. *pluricephala* occurs or did occur at one time as escaped cultivars or invasive adventives in the states of Queensland, South Australia, and Western Australia in Australia, Thailand, Tonga, and Oahu Is., Hawaii in the USA. *Solidago altissima* var. *altissima* is present in Australia and New Zealand. Semple et al. (2017) documented the presence of *S. chilensis* in Australia. The Australia's Virtual Herbarium (2017) listed 84 herbarium specimens of *S. altissima* collected in New South Wales, Queensland and Victoria, Australia. How many of these are *S. chilensis*, *S. altissima* var. *altissima*, and *S. altissima* var. *pluricephala* need to be determined.

Key to *Solidago* subsect. *Triplinerviae* taxa in Australia
All taxa in subsect. *Triplinerviae* have triple-nerved lower and middle and often upper stem leaves and have inflorescences that are generally very narrowly to broadly secund conical.

1. Lower stems hairless.

    2. Middle and upper stem leaf margins serrate, inflorescence usually nearly as wide as tall.

3. Involucres 2.5–4 mm tall at flowering .... **Solidago gigantea** (presence needs confirmation)
3. Involucres 1.7–2.5 mm tall at flowering .... **Solidago canadensis var. canadensis**

2. Middle and upper stem leaf margins entire, inflorescence much narrower than tall **Solidago chilensis**

1. Lower stems moderately to densely hairy.

4. Involucres 1.7–2.5 mm tall at flowering; upper stem leaves serrate, moderately hairy on abaxial
    main veins .... **Solidago canadensis var. hargeri**
4. Involucres 3.0–4.0 mm tall at flowering; upper stem leaves entire, densely hairy on abaxial main
    veins.

5. Infloresence about as wide as tall; upper stem leaves somewhat reduced in size compared to
    mid stem leaves .... **Solidago altissima var. altissima**
5. Infloresence narrower to much narrower than tall; upper stem leaves much reduced in size
    compared to mid stem leaves .... **Solidago altissima var. pluricephala**

ACKNOWLEDGEMENTS

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MULTIVARIATE MORPHOMETRIC CONFIRMATION
OF *SOLIDAGO CHILENSIS* (ASTERACEAE: ASTEREAE)
IN THE AZORES

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ABSTRACT
An herbarium collection of *Solidago* from near Pico Island, Azores, Portugal, is reported here to be *Solidago chilensis* Meyen. One collection (*Botelho Gonçalves 1825,* BM) was included in a multivariate morphometric analysis comparing *S. altissima, S. canadensis, S. chilensis,* and *S. gigantea.* The specimen has glabrous lower and mid stems, glabrous linear lanceolate upper stem leaves with ciliate entire margins, and secund pyramidal inflorescences that are much longer than wide.

Solidago chilensis Meyen is native to South American and is a member of *S.* subsect. *Triplinerviae* (Torr. & A. Gray) Nesom (Lopez Laphitz 2009; Lopez Laphitz & Semple, 2015). The species includes plants with densely very short canescent stems to plants with glabrous stems from base to into the inflorescence. The glabrous-stemmed morphs are most common in Argentina and occur as the only morph present in the La Plata to Buenos Aries region (Lopez Laphitz 2009); similar plants have been introduced into the West Indies and Madeira Is., Portugal (Gonçalves Silva et al. 2009) and Australia (Semple et al. 2017).

During a visit to the British Museum of Natural History (BM) in November of 2014 a specimen from Pico Island, Azores, Portugal, collected by Ilídio Botelho Gonçalves, the former director of the Serviços Florestais at Horta and Angra do Heroísmo (*Botelho Gonçalves 1825* (BM; Portugal, Autonomous Region of the Azores: Pico Is., Santo António, Ginjal, 50 m, 25 Aug 1964, Figs. 1-2) was examined and thought to be *S. chilensis* based on upper leaf traits and inflorescences shape. The specimen was subsequently borrowed for detailed study in the laboratory in Waterloo and traits scored for inclusion of the specimen in a multivariate morphometric analysis of similar plants. The specimen was originally identified as "Solidago hybrida?" then annotated by J.R. Press in October 1995 as "*Solidago gigantea* prob. subsp. *serotina* but a form with very narrow leaves." The specimen has upper stems that are glabrous even in the inflorescence and upper stem leaves that are narrowly lanceolate, trinervate, and glabrous with entire ciliate margins, which is consistent with many specimens of *S. chilensis*. The third author has collected a number of specimens from Terceira Island (Fig. 3). *Solidago gigantea* Ait. subsp. *serotina* (O. Ktze) McNeill was listed as occurring on the Azorean islands Pico, São Jorge, and Terceira in the Nova Flora do Portugal, but no specimens were cited (do Amaral Franco, 1984, Vol. II, p. 351).

Figure 1. *Solidago chilensis* from Pico Island, Azores, Portugal –– *Botelho Gonçalves 1825* (BM).
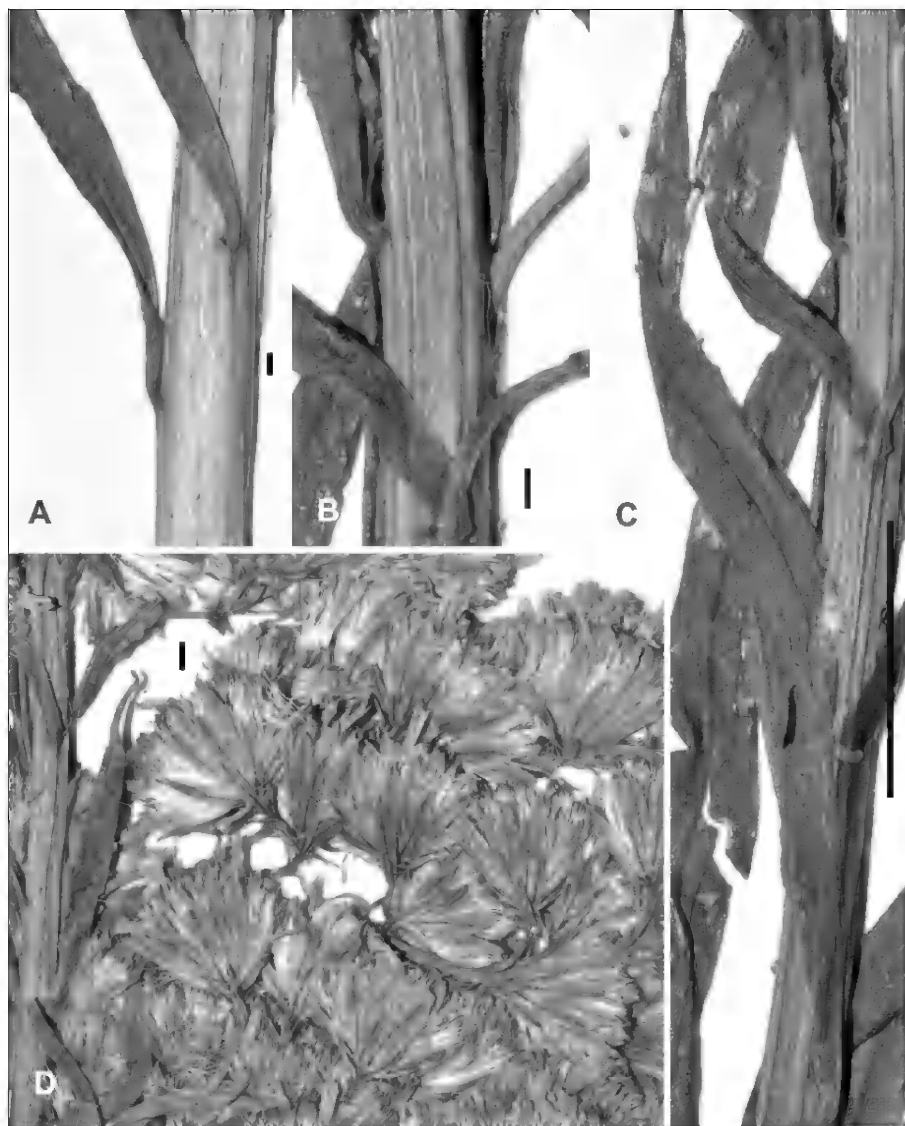
Figure 2. Details of *Solidago chilensis* from Pico Island, Azores, Portugal; *Botelho Gonçalves 1825* (BM). **A.** Upper mid stem. **B.** Upper stem just below inflorescence. **C.** Upper stem leaf, abaxial surface. **D.** Heads. Scale bar = 1 mm in A, B,and D; = 1 cm in C.

Figure 3. *Solidago chilensis* from Terceira Island, Azores, Portugal. **A-B.** Habitat and flowering shoots; Paul da Praia, Terceira, 17 Sep 2015. **C.** Dried stem and leaves; Agualva, Aug 2014. Digital images by H. Schaefer.

MATERIALS AND METHODS

Herbarium specimens of *Solidago altissima*, *S. canadensis*, *S. chilensis*, and *S. gigantea* from BM, GH, F, K, LL, LP, MADS, MEL, MO, the J.K. Morton personal herbarium now deposited in TRT, MIN, NCU, NY, PERTH, TEX, USF, and WAT in MT were used in the multivariate analyses. A list of 14 vegetative and 16 floral traits scored was included in Semple et al. (2015) and is not repeated here.

Analyses were performed using SYSTAT v.10 (SPSS 2000). A STEPWISE discriminant analysis was performed on 296 specimens of *S. altissima* (88 specimens included in Semple et al. 2015), *S. canadensis* (57 included in Semple et al. 2015), *S. chilensis* (89 specimens mostly included in Lopez Laphitz and Semple 2015), and *S. gigantea* Ait. (40 specimens, nearly all from Canada and the USA) to confirm the identification of *Botelho Gonçalves 1825* (BM) as *S. chilensis*.

RESULTS AND DISCUSSION

Because *Botelho Gonçalves 1825* (BM) was incomplete and lacked lower and mid stem portions of the shoot, only upper stem leaf traits were included. Ray floret ovary/fruit body length at anthesis and ray floret pappus length at anthesis were also not included due to high correlations with the disc floret traits.

In the STEPWISE discriminant analysis including 296 specimens in four species level a priori groups (*Solidago altissima*, *S. canadensis*, *S. chilensis* and *S. gigantea*), the following ten traits were selected as useful in separating the four a priori groups in the analysis and are presented in order of decreasing F-to-remove values: number of upper leaf margin serrations (30.59), disc corolla length (21.28), outer phyllary length (21.31), number of disc florets (18.04), upper leaf width (13.91), disc corolla lobe length (11.24), upper leaf length (10.42), disc floret pappus length at anthesis (9.53), involucre height (9.98), and disc fruit body length at anthesis (8.95). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The F-matrix for the discriminant analysis presented in Semple et al. (2017 Table 1) and is not repeated here. F-values based on Mahalanobis distances between group centroids indicated the largest separation were between *S. canadensis* and *S. chilensis* (86.564), and the least separation was between *S. altissima* and *S. canadensis* (31.180).

In the Classificatory Discriminant Analysis, correct assignments of specimens for taxa ranged from 89% to 99%. The Classification matrix and Jackknife classification matrix were presented in Semple et al. (2017 Table 2) and are not repeated here. Eighty-eight of the 89 specimens of the *Solidago chilensis* a priori group were assigned a posteriori to *S. chilensis*: *Botelho Gonçalves 1825* (BM) with 96% probability (2% to *s. gigantea* and 1% to *S. altissima*). Additional details of the results are not presented here.

Two dimensional plots of CAN1 versus CAN3 and CAN1 versus CAN2 canonical scores for 296 specimens of *Solidago altissima*, *S. canadensis*, *S. chilensis*, and *S. gigantea* are presented in Fig. 4. Eigenvalues on the first three axes were 3.625, 1.369 and 0.883.

Botelho Gonçalves 1825 (BM) is a member of *Solidago chilensis* and not *S. gigantea*. The following additional collections originally identified as *S. gigantea* are also *S. chilensis*: Portugal. Azores: Terceira, Agualva, pasture, c. 140 m, 7 Aug 2014, *H. Schaefer 2014/171*(TUM); Praia da Vitoria, *H. Schaefer 2010/478* (GH), *H. Schaefer 2014/223* (TUM); Praia da Vitoria, Paul da Praia, lake shore, ca. 10 m, 11 Sep 2013, *H. Schaefer 2013/178* (TUM). Additional herbarium collections filed as *S. gigantea* from the Azores should be examined to determine if they are also in fact *S. chilensis*. Detailed descriptions of *S. chilensis* were given in Lopez Laphitz and Semple (2015) and Semple et al. (2017).
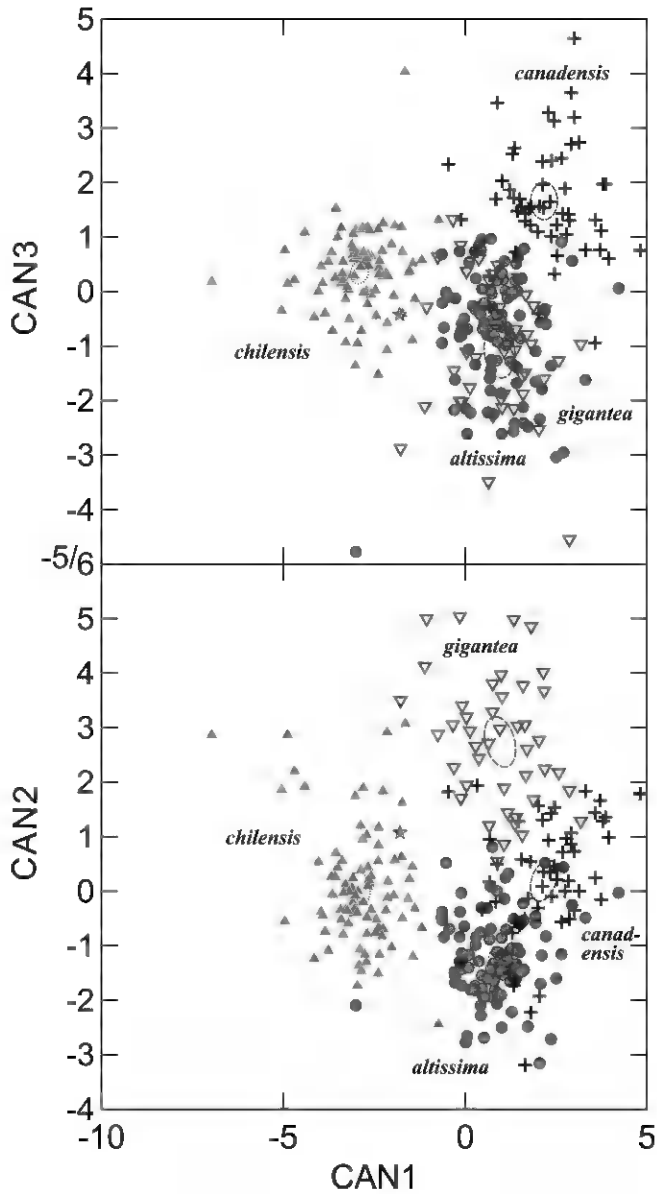
Figure 4. Plot of canonical scores CAN1 and CAN2 for specimens of *S. chilensis* (gray crosses), *S. leavenworthii* (circles), *S. microglossa* (red triangles), *Botelho Gonçalves 1825* (BM; yellow star) obtained in a discriminant analysis treating *Botelho Gonçalves 1825* (BM) as unassigned to an a priori group.

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MULTIVARIATE MORPHOMETRIC CONFIRMATION OF *SOLIDAGO CHILENSIS* (ASTERACEAE: ASTEREAE) IN AUSTRALIA

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ABSTRACT

Collections of adventive *Solidago* from the states of Western Australia, South Australia, and Victoria in Australia are reported here to be *S. chilensis* Meyen. The species is not currently listed as present in Australia. Four collections were scored and included in a multivariate morphometric analysis comparing *S. altissima*, *S. canadensis*, *S. chilensis*, and *S. gigantea* known to be adventive in Eurasia and Oceania. Additional Australian herbarium specimens not included in the analysis with glabrous lower and mid stems, glabrous linear lanceolate upper stem leaves with ciliate entire margins, and secund conical inflorescences that are much longer than wide have been determined as *S. chilensis*.

Solidago chilensis Meyen is native to South America and is a member of *S.* subsect. *Triplinerviae* (Torr. & A. Gray) Nesom (Lopez Laphitz 2009; Lopez Laphitz & Semple 2015). The species includes plants with densely very short canescent stems to plants with glabrous stems from base to into the inflorescence. The glabrous-stemmed morphs are most common in Argentina and occur as the only morph present in the La Plata to Buenos Aires region (Lopez Laphitz 2009); similar plants have been introduced into the West Indies and Madeira Island, Portugal (Conçalves Silva et al. 2009). The species is not listed as present in Australia (Australia's Virtual Herbarium 2017).

During a visit to Kew Herbarium (K; Thiers, continuously updated) in November of 2014 a specimen from Western Australia *Keighery 8049* (K; Figs. 1-2; AUSTRALIA. Western Australia: 16 km S of Perth, Jandokot, Nicholson Rd, 5 Mar 1986) was examined and thought to be either *Solidago altissima* L. var. *pluricephala* M.C. Johnst. or *S. chilensis* based on upper leaf traits and inflorescence shape. The specimen was subsequently borrowed for detailed study in the laboratory in Waterloo, Canada, and traits scored for inclusion of the specimen in a multivariate morphometric analysis of
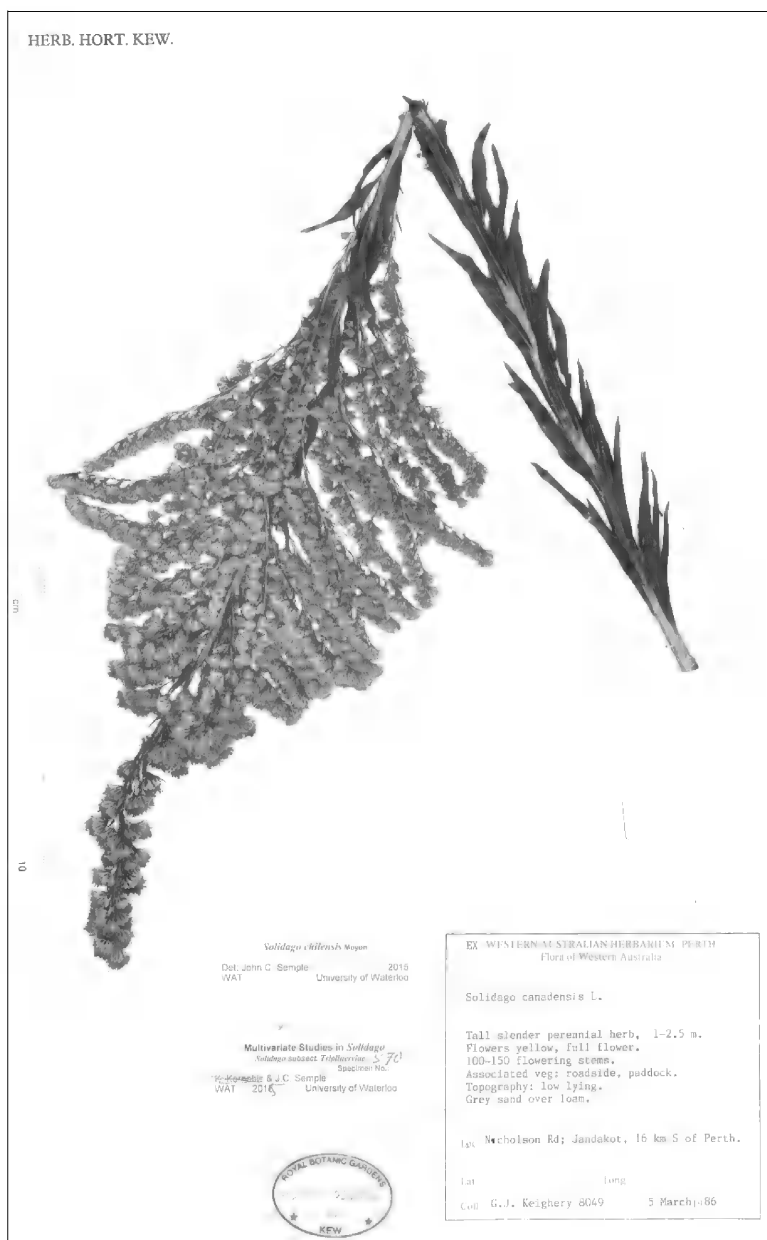
Figure 1. *Solidago chilensis* from Jandakot south of Perth, Australia; *Keighery 8049* (K).
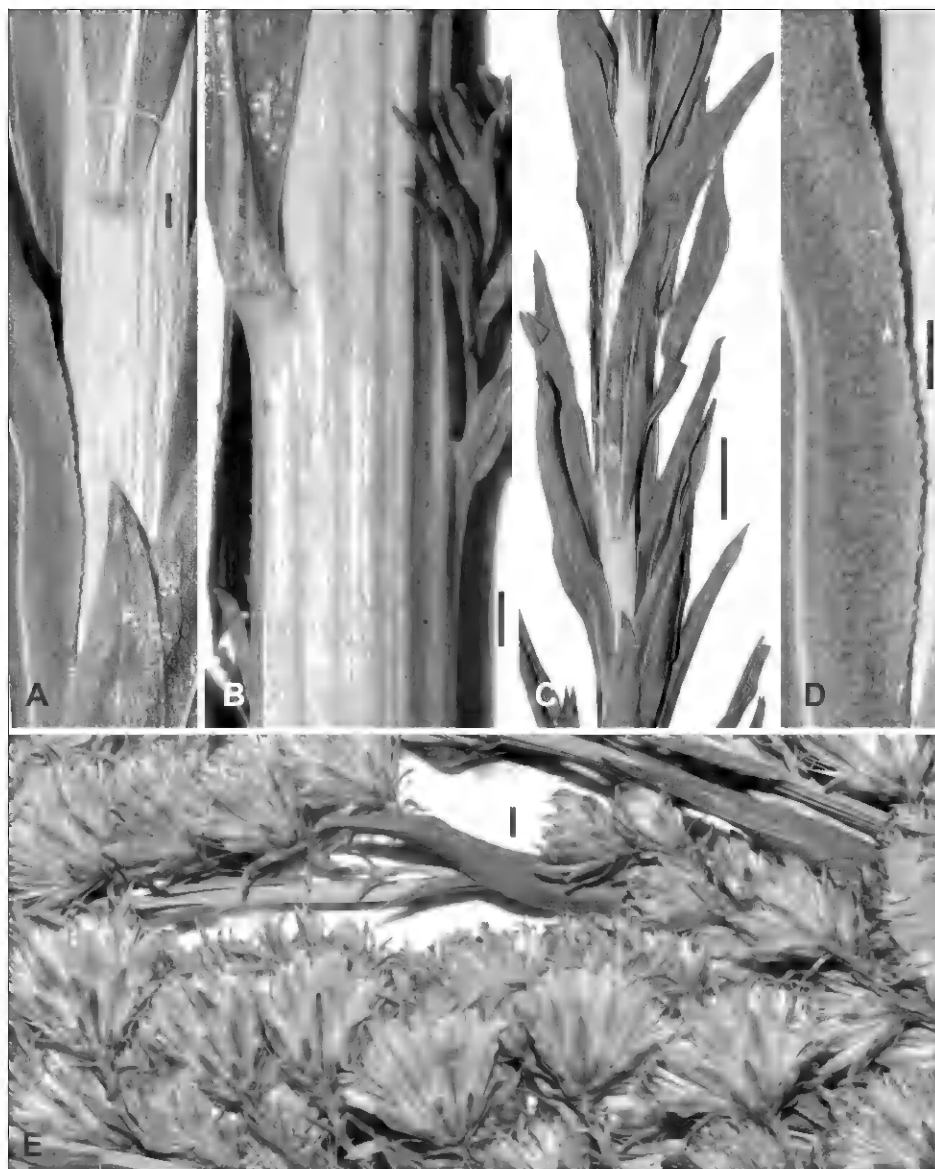
Figure 2. Details of *Solidago chilensis* from Australia, *Keighery 8049* (K). A. Upper mid stem. B. Upper stem at base of inflorescence. C. Upper stem leaves. D. Upper stem leaf , adaxial surface and ciliate margin. E. Heads. Scale bars: = 1 mm in A, B, D and E; = 1 cm in C.

similar plants. The specimen had upper stems and leaves that were glabrous or very sparsely strigose in the inflorescence which is consistent with many specimens of *S. chilensis*, but not for specimens of *S. altissima*, which is known to occur in Australia (Australia's Virtual Herbarium 2017). Additional *Solidago* specimens were borrowed from MEL and PERTH and A. Uesugi recorded data from transplanted individuals under greenhouse cultivation resulting in three additional putative *S. chilensis* collections being scored for inclusion in the multivariate analyses: *Walsh 5179* (MEL; AUSTRALIA. Victoria: Gippsland Plain, Melbourne suburb, Glen Iris, eastern bank of Gardiners Creek, 30 Mar 2000; Fig. 3), *A. Uesugi SAHV* (cult. Greenhouse, Monash University-Clayton original from AUSTRALIA. South Australia: Hope Valley, 18 May 2015), and *A. Uesugi SAPR* (cult. Greenhouse, Monash University – Clayton, originally from AUSTRALIA. South Australia: Adelaide, Player Reserve, 19 May 2015). Semple et al. (2017) noted the presence of *S. altissima* var. *pluricephala* in Australia and from several other locations in Asia, Oceania, and Hawaii. *Solidago altissima* has densely hairy stems from the base to the apex, although robust plants with thick lower stems may lose hairs as the stem grows.

MATERIALS AND METHODS

Herbarium specimens of *Solidago altissima*, *S. canadensis*, *S. chilensis*, and *S. gigantea* from BM, GH, F, K, LL, LP, MADS, MEL, MO, the J.K. Morton personal herbarium now deposited in TRT, MIN, NCU, NY, PERTH, TEX, USF, and WAT in MT were used in the multivariate analyses. A list of 14 vegetative and 16 floral traits scored was included in Semple et al. (2015) and is not repeated here.

All analyses were performed using SYSTAT v.10 (SPSS 2000). Two analysis were run to confirm the identification of *Keighery 8049* (K), *Walsh 5179* (MEL), and *Uesugi SAHV* and *Uesugi SAPR* as *S. chilensis*. A STEPWISE discriminant analysis was performed on 121 specimens of *S. chilensis* (85), *S. mexicana* (19) and *S. sempervirens* (17) to confirm that *Walsh 5179* (MEL) was not *S. mexicana* or *S. sempervirens*. A second STEPWISE discriminant analysis was performed on 296 specimens of *S. altissima* (88 specimens included in Semple et al. 2015), *S. canadensis* (57 included in Semple et al. 2015), *S. chilensis* (89 specimens mostly included in Lopez Laphitz and Semple 2015), and *S. gigantea* Ait. (40 specimens, nearly all from Canada and the USA) to confirm that *Keighery 8049* (K), *Walsh 5179* (MEL), and *Uesugi SAHV* and *Uesugi SAPR* were *S. chilensis*.

RESULTS AND DISCUSSION

Because *Keighery 8049* (K) was incomplete and lacked lower and mid stem portions of the shoot, only upper stem leaf traits were included. Ray floret ovary/fruit body length at anthesis and ray floret pappus length at anthesis were also not included due to high correlations with the disc floret traits.

In the first STEPWISE discriminant analysis including *S. chilensis*, *S. mexicana* and *S. sempervirens*, *Keighery 8049* (K), *Walsh 5179* (MEL), and *Uesugi SAHV* and *Uesugi SAPR* were all placed a posteriori into *S. chilensis* with 98-100% probability. The following five traits were selected as best separating the taxa and are listed in order of decreasing F-to-remove values: number of ray florets (74.84), upper leaf length (23.44), ray floret lamina length (21.72), number of disc florets (20.48), and involucre height (7.22). Further details of the analysis are not presented. *Walsh 5179* (MEL) was first identified as *S.* aff. *canadensis* on the original label, then annotated in 2000 from a duplicate by C. Taylor (Southeastern Oklahoma State University) as *S. sempervirens*, but was assigned a posteriori in this study to *S. chilensis* with 100% probability. At the time of performing the analysis, *Walsh 5179* (MEL) was one of 19 specimens listed under *S. sempervirens* on Australia's Virtual Herbarium: all from a narrow zone running from well north of Melbourne, to the Bass Coast south of Melbourne, Victoria. Superficially, *Walsh 5179* (MEL) looks similar to specimens of *S. sempervirens*, but on technical leaf and floret traits is clearly not that species; e g. the mid stem leaves
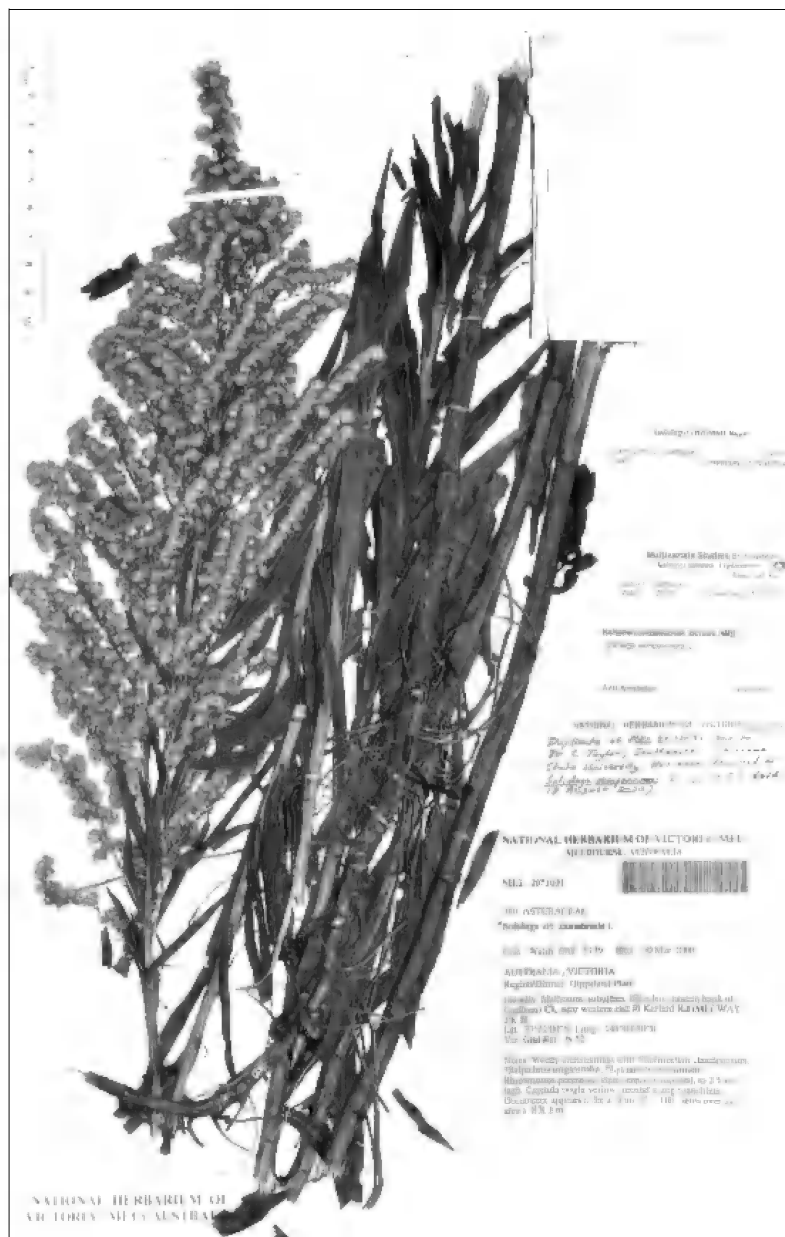
Figure 3. *Solidago chilensis* from Glen Iris, Melbourne, Australia; *Walsh 5179* (MEL).

Figure 4. *Solidago chilensis*, greenhouse-grown plant from south of greater Melbourne, Australia; *Akane Uesugi* plant SAU4 (not included in study).

Figure 5. *Solidago chilensis* in Glen Iris, Melbourne, Victoria, Australia, population near *Walsh 7159* (MEL). A. Habitat. B. Inflorescence. C. Stem leaf. Digital photographs by N.G. Walsh.

are triple-nerved.   Subsequent to submission of this publication, all of the other 18 specimens had been redetermined by N.G. Walsh to *S. chilensis*. There are no specimens at MEL or other Australian herbaria that document the presence of *S. sempervirens* in Australia.

In the second STEPWISE discriminant analysis including 296 specimens in four species level a priori groups (*Solidago altissima*, *S. canadensis*, *S. chilensis*, and *S. gigantea*), the following ten traits were selected as useful in separating the four a priori groups in the analysis and are presented in order of decreasing F-to-remove values: number of upper leaf margin serrations (30.59), disc corolla length (21.28), outer phyllary length (21.31), number of disc florets (18.04), upper leaf width (13.91), disc corolla lobe length (11.24), upper leaf length (10.42), disc floret pappus length at anthesis (9.53), involucre height (9.98), and disc fruit body length at anthesis (8.95). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 1. F-values based on Mahalanobis distances between group centroids indicated the largest separation were between *S. canadensis* and *S. chilensis* (86.564), and the least separation was between *S. altissima* and *S. canadensis* (31.180).

In the Classificatory Discriminant Analysis, correct assignments of specimens for taxa ranged from 89% to 99%. The Classification matrix and Jackknife classification matrix are presented in Table 2. Eighty-eight of the 89 specimens of the *Solidago chilensis* a priori group were assigned a posteriori to *S. chilensis*: *Keighery 8049* (K) with 100% probability, *Walsh 5179* (MEL) with 98% probability, *Uesugi SAHV* with 95% probability, and *Uesugi SAPR* with 68% probability (30% to *S. altissima* and 2% to *S. gigantea*; this was a greenhouse grown specimen). Additional details of the results are not presented here.

Table 1. Between groups F-matrix for the four a priori groups analysis (df = 10 283).

Group	altissima	canadensis	chilensis
canadensis	31.180		
chilensis	74.882	86.564	
gigantea	38.706	33.039	57.985

Wilks's lambda = 0.0485 df = 10 3 292; Approx. F= 49.9922 df = 30 831   prob = 0.0000

Table 2. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of four a priori groups; a posteriori placements to groups in rows.

Group	altissima	canadensis	chilensis	gigantea	% correct
altissima	100	7	1	2	91
canadensis	3	51	0	3	89
chilensis	1	0	88	0	99
gigantea	0	1	1	38	95
Totals	104	59	90	43	94

Jackknifed classification matrix

Group	altissima	canadensis	chilensis	gigantea	% correct
altissima	100	7	1	2	91
canadensis	6	48	0	3	84
chilensis	1	1	86	1	97
gigantea	1	1	3	35	88
Totals	108	57	90	41	91

Two dimensional plots of CAN1 versus CAN3 and CAN1 versus CAN2 canonical scores for 296 specimens of *Solidago altissima*, *S. canadensis*, *S. chilensis*, and *S. gigantea* are presented in Fig. 5. Eigenvalues on the first three axes were 3.625, 1.369 and 0.883.

Additional collections of *S. chilensis* examined. **AUSTRALIA**. **Victoria**: Balwyn North, brow of the S bank of Koonung Creek, adjacent to the NE corner of the Boroondara Tennis Centre car park, 19 Apr 2005, *Lorimer 1886a* (MEL); Echuca Village, Mitchell Road, 29 Mar 2004, *Caldwell s.n.*, (MEL); Inverloch, south side of Esplanade, opposite intersection with Nautilus Rd., 16 Mar 2008, *Stajsic 4498* (BRI, MEL, NSW); Inverloch, foreshore, 20 Mar 2006, *Hibbert s.n.* (MEL). **Western Australia**: Bayswater, Baigup Wetlands, 3 Mar 1999, *Keighery 15665* (PERTH); Bayswater, NW bank of Swan River at Garratt Rd Bridge, 6 Mar 1995, *Lepschi & Lally 1755* (AD, CANB, PERTH), W end of Garret Rd Bridge, 3 Jul 2001, *Davis 9816* (PERTH); Brookton Hwy, 0.5 km from Croyden Rd, s.d., *Lloyd s.n.* (PERTH); Canning Vale, Randford Rd., 500 m E of Nicholson Rd, s.d., *Lloyd s.n.* (PERTH); ca 14 km SSE of Capel on road to Donnybrook, 3 May 1996, *Lepschi & Lally BJL 2592* (AD, CANB, PERTH, US); Esperance, 4 Mar 1999, *Turley 5/399* (PERTH); Dempster St, vacant lot, 4 Apr 1987, *Keighery & Alford 1307* (PERTH); Lake Richmond Nature Reserve, NE side, 100 m from Safety Bay Rd, 20 Apr 2001, *Bellman 6* (PERTH); Wembley Downs, near junction of Weaponess Road and Empire Ave, 29 Mar 2000, *Davis 9153A* (PERTH).

Almost certainly, additional collections of *S. chilensis* are included among the 196 specimens of *Solidago* listed on Australia's Virtual Herbarium (2017).
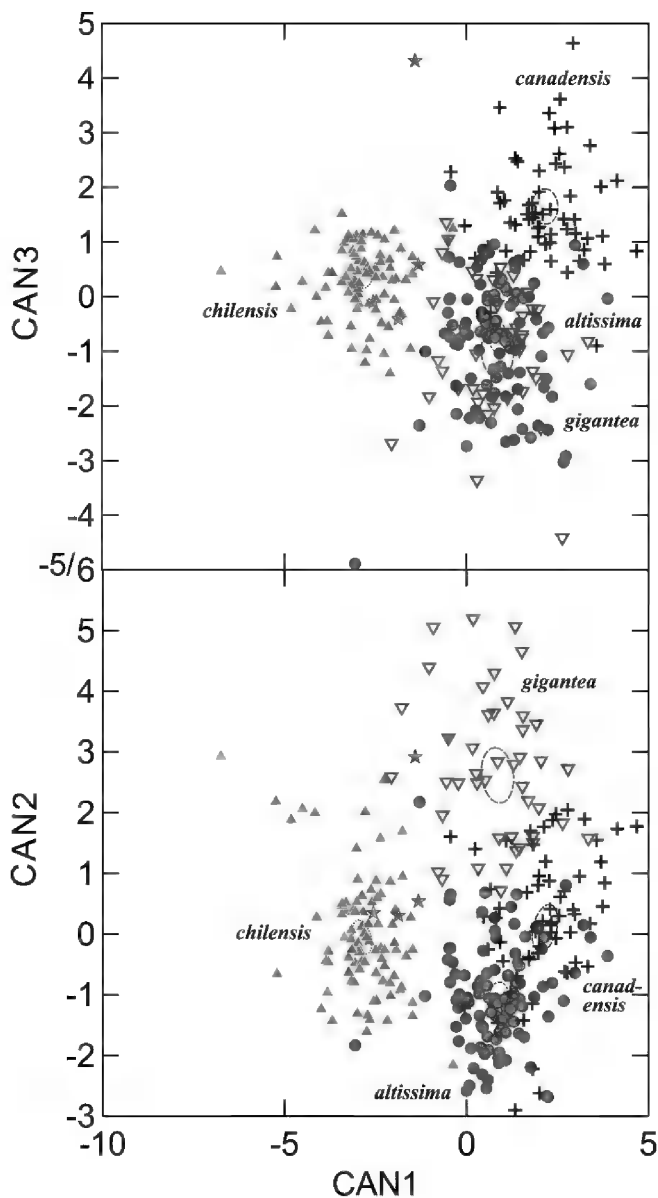
Figure 4. Plot of canonical scores (CAN1 vs CAN3 and CAN1 vs CAN2) for 296 specimens of adventive species of *Solidago*: *S. altissima* (red dots), *S. canadensis* (black +s), *S. chilensis* (blue triangles; Australian adventives-yellow stars), and *S. gigantea* (green inverted open triangles).

Detailed description of *Solidago chilensis* based on all collections included in the analyses
(modified from Lopez Laphitz and Semple 2015; means in bold face)

Herbaceous perennials from short to long rhizomes; stems 7–**105**–200 cm, erect, glabrate proximally, glabrate to densely canescent distally, hairs 0.05–0.3 mm. Leaves with the proximal ones oblanceolate, twisted, nearly always withering well before flowering; mid-stem leaves usually persisting, in most cases the biggest, sessile, blades linear to oblanceolate, 13–**61**–130 × 2–**6.7**–32 mm, with 0–**2**–12 serrations, 3(5)-nerved from shortly above base, abaxial and adaxial faces glabrous or sparsely strigose; distal leaves linear-lanceolate, smaller than proximal, 10–**37**–80 × 1–**4**–27 mm, with 0–**0.5**–10 serrations; inflorescence leaves linear to lanceolate, 4.4–**45** × 0.5–18 mm with 0–5 serrations. Heads 20 to 200 plus; in secund lax to dense conical paniculiform arrays, 5–**13.8**–32 × 1–**7.9**–35 cm, branches spreading recurved, secund; involucres campanulate, 3.5–**4.4**–5.5 m high; phyllaries in 3 or 4 series, those of outer series ovate, 1.1–2.7 × 0.3–1.6 mm, with inner phyllaries oblanceolate, 0.29–5.1 × 0.3–1 mm, 1 to 3 nerves. Ray florets 7–**14**–21; laminae yellow, 0.4–**2.9**–3.1 × 0.1–**0.5**–1.2 mm; disk florets 2–**9**–30; corollas 2.4–**3.8**–4.9 mm, lobes 0.12–**1.1**–3.9 mm. Fruit: cypselae body, 0.6–**0.8**–1.5 at anthesis, to 3.3 mm at maturity, sparsely to densely strigose; longest pappus bristles 1.9–**3.5**–5.1 mm. Chromosome count 2n = 18.

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EUPATORIUM CAPILLIFOLIUM (ASTERACEAE) NEW TO NEW YORK

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ABSTRACT

Eupatorium capillifolium (Asteraceae) is reported new to the flora of New York based on a 2015 collection from eastern Long Island, Suffolk County, and observations from 2013 to 2017.

Recent field work on eastern Long Island has revealed a population of *Eupatorium capillifolium* (Lam.) Small from Suffolk Co., New York. The species was not included in the flora of New York by Torrey (1843), House (1924), Mitchell (1986), Mitchell and Tucker (1997), Siripun and Schilling (2006), Weldy et al. (2016), or USDA PLANTS database (USDA, NRCS 2017). We report our voucher collection of *E. capillifolium*, documenting the first known persisting population of this species from the state.

Eupatorium capillifolium (Lam.) Small ex Porter & Britton, Mem. Torrey Bot. Club 5: 311. 1894.

Voucher: **USA**. **New York.** Suffolk Co.: Southampton Township, 2.7 km (by air) SW of Riverhead, between Routes 24/25 and Route 27, Wildwood Lake Town Park, 40.895829°N, 72.677918°W (WGS84, ±25m), 2 m elev., 7 Oct 2015, *Lamont s.n.* (NY). Figure 1.

The population, located by Feder in 2013, consists of a discrete cluster of stems located along the upland border of a shallow cove on the northwest section of Wildwood Lake (Figure 2). The open, sandy habitat is dominated by herbs and shrubs including *Eupatorium hyssopifolium, Panicum virgatum, Euthamia caroliniana, Solidago odora, Erigeron canadensis* var. *canadensis, Artemisia vulgaris, Morella caroliniensis, Ilex glabra, Vaccinium corymbosum,* and *Clethra alnifolia.* The population has been monitored from 2013 to 2017 and a cursory search of adjacent areas revealed no additional individuals of *E. capillifolium* although suitable habitat was abundant. In 2017 Lamont counted 16 stems, perhaps representing a single clone. Stems and leaves first emerge in early to mid-May and flower buds begin to form in late September or early October with anthesis continuing into mid-November.

We consider the nativity status of *Eupatorium capillifolium* in New York to be "unknown" because the origin of the Long Island population cannot be determined as natural or a result of human assistance.

Eupatorium capillifolium is one of three wind-pollinated species [*E. compositifolium* Walt., *E. leptophyllum* DC.] in the genus from North America north of Mexico (Siripun & Schilling 2006). All three species occur on the Atlantic coastal plain and only *E. capillifolium* ranges north of North Carolina. Throughout its range on the Atlantic coastal plain *E. capillifolium* has been described as "aggressive and weedy" (Fernald 1950), occurring in open places including roadsides, clearings, old fields and pastures, disturbed woods, borders of woods, flatwoods, marshes, and wet disturbed sites

Figure 1. *Eupatorium capillifolium* from Suffolk Co., New York (*Lamont s.n.*, NY).

Figure 2. Habitat of *Eupatorium capillifolium* bordering Wildwood Lake, Suffolk Co., New York (10 Nov 2016). Arrow points to discrete cluster of about a dozen stems of *E. capillifolium.*

(Fernald 1950; Radford et al. 1968; Cronquist 1980; Wunderlin 1998). Because this species occurs in disturbed and undisturbed habitats, determining its nativity can be difficult in newly colonized sites just beyond its historical range limit.

Historically, southern New Jersey (Cape May Co.) was considered the northern range limit of *Eupatorium capillifolium* (Cronquist 1980; Hough 1983) but during the past 30 years it has colonized the coastal plain north to Burlington Co. (G. Moore and T. Gordon, pers. comm.). The species has been reported from Connecticut and/or Massachusetts by Fernald (1950), Siripun and Schilling (2006), and USDA PLANTS database (USDA, NRCS 2017) although the species was not included in the flora of New England by Haines (2011).

In New York, *Eupatorium capillifolium* was reported in 1997 from Staten Island (Richmond Co.) based on a misidentified collection of *Artemisia campestris* subsp. *caudata* (8 Oct 1991, *Meyer s.n.*, SIM!); Fernald (1950) described *E. capillifolium* as "superficially suggesting *Artemisia.*" In 2008, *E. capillifolium* was reported as unintentionally introduced by humans in Kings Co., but it did not persist (Tudor et al. 2015).

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FOUR NEW SUBTRIBES: ALLOLEPIINAE, JOUVEINAE, KALINIINAE, AND SOHNSIINAE IN THE CYNODONTEAE (POACEAE: CHLORIDOIDEAE)

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ABSTRACT

Allolepis, Jouvea, Kalina, and *Sohnsia* are small (only *Jouvea* contains two species), often overlooked genera that are morphologically and genetically isolated within the tribe Cynodonteae. We present a molecular phylogeny using sequence data from seven plastid markers (*ccsA, ndhA* intron, *ndhF, rpl32-trnL, rpoC2, rps16-trnK,* and *rps16* intron) and the nuclear ribosomal internal transcribed spacer regions (ITS 1 & 2). Since *Allolepis, Jouvea, Kalinia,* and *Sohnsia* do not align within any of the 21 existing Cynodonteae subtribes, we describe **Allolepiinae**, **Jouveinae**, **Kaliniinae**, and **Sohnsiinae** as new. In addition, we provide descriptions, habitat, distribution, and comments for each subtribe.

Allolepis texana (Vasey) Scribn., *Jouvea pilosa* (J. Presl) Scribn, *J. straminea* E. Fourn., and *Sohnsia filifolia* (E. Fourn.) Airy Shaw are dioecious, caespitose grasses, whereas *Kalinia obtusiflora* (E. Fourn.) H.L. Bell & Columbus has 4–8 mm wide, sharp-pointed rhizomes and perfect florets. Historically, these western hemisphere grasses were placed in other genera, i.e., *Brizopyrum* (Presl, 1830; Fournier 1886)*, Calamochloa* (Fournier 1877), *Distichlis* (Lamson-Scribner 1899)*, Eragrostis* (Lamson-Scribner 1897)*, Poa* (Kunth 1833; Vasey 1890b), and *Rhachidospermum* (Vasey 1890a), until recently being aligned within the Cynodonteae (Columbus 2007; Peterson et al. 2010, 2016). An early molecular phylogeny of the subfamily Chloridoideae placed *Allolepis, Jouvea*, and *Sohnsia* within the tribe Cynodonteae (Columbus et al. 2007). Later molecular studies have confirmed that these three genera, along with *Kalinia*, are members of the supersubtribe Bouteluouodinae, a primarily Western Hemisphere clade within the Cynodonteae that includes six subtribes: Boutelouinae, Hilariinae, Monanthochloinae, Muhlenbergiinae, Scleropogoninae, and the Traginae (Bell et al. 2013; Peterson et al. 2010; 2016; Soreng et al. 2017). However, these four genera do not align within any of the existing 21 subtribes of Cynodonteae (Peterson et al. 2010; 2016; Soreng et al. 2017) or within the six subtribes of Bouteluouodinae. *Allolepis, Jouvea*, and *Sohnsia* are strictly dioecious whereas *Kalinia* is hermaphroditic. All four genera are endemic or centered in México (one extending into Texas, another into Arizona and New México, one other extending south to Panama in Central America, and Ecuador in South America), emphasizing the morphological diversification of the Bouteluouodinae in this region and the correlation of outcrossing breeding systems with this diversification. We present a molecular phylogeny using sequence data from seven plastid markers (*ccsA, ndhA* intron, *ndhF, rpl32-trnL, rpoC2, rps16-trnK,* and *rps16* intron) and a single nuclear marker (ITS) emphasizing these four genera, and describe four new, monotypic subtribes within the Bouteluouodinae.

MATERIALS AND METHODS

The phylogram (Fig. 1) was generated with existing data from Peterson et al. (2010, 2016) and we added three samples, one for *Allolepis, Jouvea pilosa*, and *Sohnsia*. Voucher information and GenBank numbers for the four genera are given in Table 1. The methods for DNA extraction, primers, amplification, sequencing, and phylogenetic analysis are given in Peterson et al. (2010, 2016). We estimated the phylogeny among members of these four genera and the Cynodonteae based on the analysis of eight molecular markers (nuclear ITS 1&2 and plastid *ccsA, ndhA* intron, *ndhF, rpl32-trnL, rpoC2, rps16-trnK*, and *rps16* intron DNA sequences). To make the phylogram smaller, taxa already placed in existing subtribes or tribes are depicted only at that level.
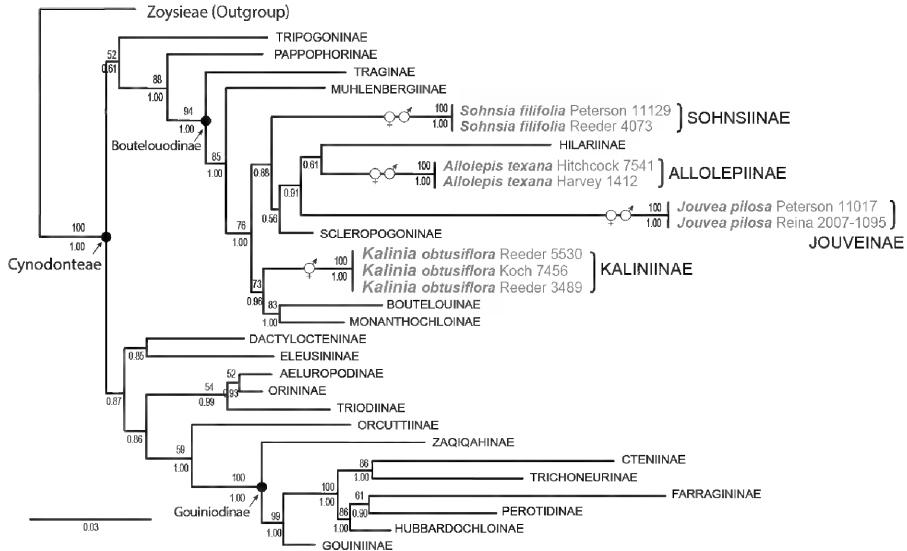
Figure 1. Maximum-likelihood tree inferred from combined plastid (*ccsA, ndhA* intron, *ndhF, rpl32-trnL, rpoC2, rps16-trnK*, and *rps16* intron) and ITS sequences. Numbers above branches are bootstrap values; numbers below branches are posterior probabilities; vertical bars indicate our classification; circle with a cross = female plants; circle with an arrow = male plants; circle with cross and arrow indicates plants with perfect flowers; scale bar = 3%.

RESULTS AND DISCUSSION

The maximum-likelihood tree from the combined analysis of seven plastid regions *ccsA, ndhA* intron, *ndhF, rpl32-trnL, rpoC2, rps16-trnK*, and *rps16* intron) and ITS depicts *Allolepis, Jouvea, Kalinia*, and *Sohnsia* in separate clades embedded within the supersubtribe Boutelouinae clade (Fig. 1). The species within each of the four genera form strongly supported clades [bootstrap (BS) = 100, posterior probability (PP) = 1.00]. *Kalinia* is moderately supported as sister to the Boutelouinae–Monanthochloinae clade (BS = 73, PP = 0.96). *Allolepis* is unsupported as sister to the Hilariinae (PP = 0.61), *Jouvea pilosa* is unsupported as sister to the *Allolepis*–Hilariinae clade (PP = 0.91), and *Sohnsia* is unsupported as sister to the Scleropogoninae–*Jouvea*–*Allolepis*–Hilariinae clade. Successive sisters to the aforementioned lineage are the Muhlenbergiinae (near, BS = 76, PP = 1.00) and the Tragiinae (next, PP = 85, PP = 1.00). The Cynodonteae phylogeny based on analysis of 389 samples in 213 species presented in Peterson et al. (2016) is identical with our new phylogeny.

Table 1. List of sampled specimens of the genera *Allolepis*, *Jouvea*, *Kalinia*, and *Sohnsia*; taxon voucher (collector, number; all specimens housed at the United States National Herbarium), country and state of origin, and GenBank accession for DNA sequences is given.

Taxon	Voucher	Country	ITS	ccsA	ndhA intron	ndhF	rpl32-trnL	rpoC2	rps16-trnK	rps16 intron
Allolepis texana (Vasey) Soderstr. & H.F. Decker	Hitchcock 7541	México, Durango	GU359264	JQ345048	GU359388	GU359577	GU360015	–	GU360573	GU360318
Allolepis texana (Vasey) Soderstr. & H.F. Decker	Harvey 1412	México	GU359265	–	GU359387	GU359588	GU360016	–	GU360572	GU360306
Jouvea pilosa (J. Presl) Scribn.	Peterson 11017 & Annable	México, Colima	GU359144	JQ345095	GU359433	GU359737	GU359812	KX582800	GU360696	GU360379
Jouvea pilosa (J. Presl) Scribn.	Reina 2007-1095, Van Devander, Chamberland & Bertelsen	México, Sonora	KJ768884	KX582279	KX582475	KX582538	KJ768979	KX582801	KX582972	KX582905
Kalinia obtusiflora (E. Fourn.) H.L. Bell & Columbus	Koch 7456	México, Lago de Texcoco	KX582380	–	–	KX582539	KX582656	–	KX582973	KX582906
Kalinia obtusiflora (E. Fourn.) H.L. Bell & Columbus	Reeder 3489, Reeder & Soderstrom	México, Chihuahua	KX582381	–	–	KX582540	KX582657	–	KX582974	KX582907
Kalinia obtusiflora (E. Fourn.) H.L. Bell & Columbus	Reeder 5530 & Reeder	USA, Arizona	KX582382	–	–	KX582541	KX582658	–	KX582975	KX582908
Sohnsia filifolia (E. Fourm.) Airy Shaw	Peterson 11129 & Annable	México, San Luis Potosi	GU359204	JQ345145	GU359531	GU359612	GU359918	KX582839	GU360634	GU360350
Sohnsia filifolia (E. Fourm.) Airy Shaw	Reeder 4073 & Reeder	México	GU359205	–	GU359532	GU359614	GU359917	–	GU360633	GU360332

In the taxonomy section below we describe each of these four genera as subtribes (Allolepiinae, Jouveinae, Kaliniinae, and Sohnsiinae) since they do not align within any existing Cynodonteae subtribes.

In the Boutelouodinae, dicliny occurs in the Allolepiinae, Boutelouinae (*Bouteloua*), Jouveinae, Monanthochloinae (*Distichlis*), Scleropogoninae (*Blepharidachne, Munroa,* and *Scleropogon*), and the Sohnsiinae. There are at least 15 diclinous species found in four sections of *Bouteloua*: *Buchloe, Cyclostachya, Opizia,* and *Triplathera* (Kinney et al. 2007; Peterson et al. 2015; Schrager-Lavelle et al. 2017). Within Chloridoideae, dicliny is apparently restricted to the western hemisphere (Connor 1979).

TAXONOMY

Allolepiinae P.M. Peterson, Romasch., & Y. Herrera, **subtribe nov.**

    TYPE: *Allolepis* Soderstr. & H.F. Decker, Madroño 18: 36. 1965.

    Dioecious, caespitose perennials with stolons 5–25 cm long, 1–4 mm wide. **Culms** 10–70 cm tall. **Leaf** sheaths shorter than flowering culm internodes with smooth margins; ligules 0.5–1.4 mm long, a ciliate membrane; blades 5–30 cm long, 2.5–6 mm wide, sometimes involute towards apex. **Panicles** 3–23 cm long, 1–6 cm wide, narrow; primary branches appressed to main axis (usually floriferous to base), terminating in a spikelet with appressed secondary branches; pedicels glabrous, smooth; disarticulation above glumes, lemma and palea falling as a unit; rachilla glabrous. **Staminate** spikelets 9–23 mm long, 3–8 mm wide, 4–14(–20)-flowered, ovate to lanceolate-linear, solitary, stramineous, terete, coriacious; glumes 4–5 mm long, broadly ovate; lower glumes 1-veined; upper glumes 1 or 3-veined, a little longer than the lower; lemmas 5–5.5 mm long, 3-veined, glabrous, shiny; paleas equal or slightly longer than the lemma; stamens 3, anthers 3–3.5 mm long, yellow. **Pistillate** spikelets 10–30 mm long, 2.5–3.5 mm long, 5–10-flowered, slightly laterally compressed with sterile florets present above fertile, coriaceous; glumes 5–12 mm long, glabrous; lower glumes 5–10 mm long, 1-veined with 4 or 5 additional faint veins; upper glumes 6–12 mm long, 3-veined, sometimes with 2 or 4 additional faint veins; lemmas 5–11 mm long, 3-veined, coriaceous, glabrous, midvein scabrous above, margins irregular and scarious; paleas slightly shorter than the lemma, keels ciliolate; lodicules 3, cuneate; stigmas 2. **Caryopsis** ellipsoid, with a fused pericarp adherent. $2n = 40$ (Gould, 1966).

    Included taxon—*Allolepis texana* (Vasey) Soderstr. & H.F. Decker [syn. *Poa texana* Vasey; *Sieglingia wrightii* Vasey; *Distichlis texana* (Vasey) Scribn.].

    Habitat—Sandy and silty soils but not in alkaline areas; 900–2000 m.

    Distribution—Known from the Big Bend region of southwestern Texas, USA (Jeff Davis and Presidio counties) and Chihuahua, Coahuila (Municipio Satillo), Durango (Municipio Ocampo), and Tamaulipas, México (Powell 1994). Based on a *Hitchcock 7541* (US-913782, US-913783) collection label that states "Torreón, Durango," this species was reported as occurring in Durango by Soderstrom and Decker (1965) and Powell (1994). *Hitchcock 7540* was collected from Torreón-Durango border and *Hitchcock 7542 & 7543* was also collected from Torreón, Durango. It seems likely that Hitchcock knew what state he was in, and collected these plants in Torreón de Cañas, Durango and not Torreón, Coahuila.

    Comments—Vasey (1890b) first described this *Allolepis texana* in *Poa* L. and later, based on a different collection, described the same species in *Sieglingia* Bernh. (Vasey 1893). Based on having a dioecious habit, a paniculate inflorescence, subcoriaceous glumes, exserted styles, and grains enclosed by a palea base, Lamson-Scribner (1899) transferred this species to *Distichlis*. *Allolepis* is very similar to *Distichlis*, sharing the dioecious habit, a ciliate membrane for a ligule, disarticulation above the glumes, and many florets per spikelet (Clayton & Renvoize 1986; Peterson

et al. 1995, 1997). Soderstrom and Decker (1965) found that *Allolepis* can be distinguished from *Distichlis* in having stolons and the absence of rhizomes, non-distichous leaf blade arrangement, heteromorphic staminate and pistillate spikelets, non-sunken bicellular microhairs, and occurrence in sandy soils (not alkaline).

Jouveinae P.M. Peterson, Romasch., & Y. Herrera, **subtribe nov.**

TYPE: *Jouvea* E. Fourn., Bull. Soc. Roy. Bot. Belgique 15: 475. 1876.

Dioecious, caespitose perennials with stolons, often with scaly buds. **Culms** 20–60 cm tall, decumbent or mat forming, glabrous. **Leaf** sheaths shorter or longer than internodes with smooth margins; ligules 0.5–1 mm long, a line of hairs; blades 1–15 cm long, 1–4 mm wide, flat becoming involute, pungent. **Inflorescences** 2–3 cm long, of 1-many spikelets in fascicles of 1–5 in pistillate plants; inflorescence a panicle 2–6 cm long in staminate plants; inflorescence exserted (smooth in staminate plants) or fully included (pistillate plants spikelets are embedded in sponge-like tissue of rachilla, only summit of florets free); primary branches appressed to main axis terminating in a spikelet; disarticulation above the glumes, lemma and palea falling as a unit. **Spikelets** 8–40 mm long (15–40 mm long in staminate spikelets) or in clusters (pistillate spikelets), (3–)5–25-flowered, laterally compressed, sessile, sterile florets present about fertile florets; rachilla glabrous; glumes present or absent, shorter than spikelets (in staminate spikelets), smooth, glabrous; lower glume unveined; upper glume shorter than lower lemma, 1-veined; lemmas 3-veined, coriaceous, glabrous, smooth; paleas chartaceous, glabrous, smooth, margins not enfolding the fruit; lodicules absent; stamens 3 or rudimentary, anthers yellow or reddish purple; stigmas 2 or rudimentary, exserted. **Caryopsis** ellipsoid, terete, with a fused pericarp. $2n = 20$ (Pohl & Davidse 1971)

Included taxa—*Jouvea pilosa* (J. Presl) Scribn. [syn. *Brizopyrum pilosum* J. Presl; *Poa preslii* Kunth; *Rhachidospermum mexicanum* Vasey]; *Jouvea straminea* E. Fourn.

Habitat—Near the immediate coast on sand dunes and unprotected beaches forming densely foliaceous mounds (*J. pilosa*) and in saline mud flats forming loosely interspersed culms (*J. straminea*) [Pohl & Davidse 1994].

Distribution—The genus occurs in México (Baja California Sur, Chiapas, Colima, Guerrero, Jalisco, Michoacán, Nayarit, Oaxaca, Sinaloa, Sonora), Central America (Costa Rica, El Salvador, Guatemala, Honduras, Nicaragua, Panama), and Ecuador (*J. straminea*) [Pohl & Davidse 1994; Espejo Serna et al. 2000; Dávila et al. 2006].

Comments—Pilger (1956) recognized the unique morphological features by erecting the tribe Jouveeae Pilg. (Pilger 1956), referring to Weatherwax's (1939) comments, "but the weight of evidence at present favors placement in the Festuceae." Although Weatherwax did indicate that the staminate spikelets of *Jouvea* resembled those found in *Distichlis*. Pistillate plants are characterized by an inflorescence that consists of 2–5 spikelets embedded in a sponge-like tissue of the rachilla, with only the summit of the florets free (Peterson et al. 1997). Clayton and Renvoize (1986) placed *Jouvea* near *Distichlis* in the Monanthochloinae as treated then along with *Allolepis* and *Swallenia* Soderstr. & H.F. Decker. *Jouvea* and *Distichlis* share distichously arranged leaves and the dioecious habit (Peterson et al. 1997). Molecular studies clearly place *Swallenia* within the Scleropogoninae (Peterson et al. 2010; 2016).

Kaliniinae P.M. Peterson, Romasch., & Y. Herrera, **subtribe nov.**

TYPE: *Kalinia* H.L. Bell & Columbus, Aliso 30(2): 91–93, f. 9. 2012.

Hermaphroditic perennials with scaly, sharp-pointed rhizomes, with innovations, sometimes stoloniferous, the sharp-tipped rhizomes 4–8 mm thick. **Culms** 15–40(–50) cm tall, erect, stiff, hard, glaucous below the nodes. **Leaf** sheaths hairy at the apices, hairs to 2 mm long; ligules 0.2–0.4 mm

long, membranous, ciliate; blades 2–15 cm long, (1–)2–4 mm wide, involute, arcuate, glabrous abaxially, scabrous adaxially, apices sharply pointed. **Panicles** 6–20(–24) cm long, 2–8(–12) cm wide, ovate, open or contracted; primary branches 1–8(–15) cm long, appressed or diverging up to 50° from the rachises; pedicels 0–8 mm long, appressed, lower pedicels on each branch shorter than 1 mm long. **Spikelets** 8–14 mm long, 1.4–3 mm wide, ovate to lanceolate, stramineous with a reddish-purple tinge, with 5–10 florets; disarticulation basipetal, glumes 1(3)-veined, persistent; glumes unequal, chartaceous; lower glumes 2.4–3.6 mm long, 1-veined; upper glumes 3–4.5 mm long, sometimes 3-veined; lemmas 3.8–4.5 mm long, ovate, leathery, 3-veined, lateral veins evident, greenish, upper margins hyaline, apices acute to obtuse, usually erose; paleas 3.8–4.5 mm long, membranous, keels scabridulous, apices obtuse to truncate; stamens 3, anthers 2–2.4 mm long, purplish to yellowish. **Caryopses** 1.6–2 mm long, ellipsoid, with a fused pericarp, dorsally flattened, with a shallow adaxial groove, striate, reddish-brown. $2n = 40$ (Reeder 1977).

    Included taxon—*Kalinia obtusiflora* (E. Fourn.) H.L. Bell & Columbus [syn. *Brizopyrum obtusiflorum* E. Fourn., Mexic. Pl. 2: 120. 1886; *Eragrostis obtusiflora* (E. Fourn.) Scribn.].

    Habitat—It grows in dry or wet alkali flats and playas, often in association with *Distichlis* and *Sarcobatus*; 900–1400 m.

    Distribution—*Kalinia obtusiflora* is native to the USA in southeastern Arizona and southwestern New México and occurs in the following Mexican states: Chihuahua (municipios Ascensión and Saucillo), Coahuila, Distrito Federal, Guanajuato, Jalisco, México (municipios Ecatepec de Morelos, Montecillo, Texcoco, and Tezoyuca), Michoacán (Municipio Cuitzeo), Nuevo León, Oaxaca, Sonora (municipios Bacoachi and Cananea), and Veracruz (Espejo Serna et al. 2000; Peterson 2003; Dávila et al. 2006; Valdés Reyna 2015).

    Comments—The type species was first described by Fournier (1886) in *Brizopyrum* Link along with other species that are now included in *Distichlis* (= *D. spicata* subsp. *stricta* Thorne), *Jouvea*, and *Uniola* (*U. pittieri* Hack.). Ogden (1897) performed an anatomical survey of four grasses, *Kalinia obtusiflora, Jouvea pilosa, J. straminea*, and *Distichlis spicata* (L.) Greene, all inhabitants of saline environments in southwestern North America. Ogden had originally thought that *Kalinia obtusiflora* was conspecific with *Jouvea*. While all three of these species appear to be C$_4$ NAD-ME grasses, there are few unique anatomical features among each of these species (Peterson et al. 2005). *Kalinia obtusiflora* has a crown of colorless cells above each vein that is absent from the other three genera. Even though Fournier (1886) and later Ogden (1896) noticed affinities of *Kalinia* with *Distichlis, Jouvea*, and *Uniola*, all American agrostologists have followed Lamson-Scribner's (1897) placement of this species in *Eragrostis* until Bell et al. (2013) erected *Kalinia* for it. *Kalinia* appears to differ from other species of *Eragrostis* in having leaf blades with papillae located in the intercostal zones on the abaxial surface, stomata on the lemma surface, and the lack of interruption of the bundle sheath with sclerenchyma (known in *E. pergracilis* S.T. Blake) [Bell et al. 2013]. Bell et al. (2013) also found that *Kalinia* differs from *Distichlis* in having a bundle sheath extensions of colorless cells (absent in *Distichlis*) and wide metaxylem cells (narrow in *Distichlis*). *Distichlis* and *Kalinia* do share sunken bicellular microhairs on the surface of the leaf blades (Bell et al. 2013).

Sohnsiinae P.M. Peterson, Romasch. & Y. Herrera, **subtribe nov.**

    Type: *Sohnsia* Airy Shaw, Kew Bull. 18(2): 272. 1965.

    Dioecious, caespitose perennials with short rhizomes forming tough clumps. **Culms** 30–100 cm tall, pubescent below the nodes. **Leaf** sheaths sometimes auriculate, hairy at summit margins; ligules 0.7–1.1 mm long, a line of hairs; blades flat becoming involute upon drying, antrorsely scabrous. **Panicles** 7–21 cm long with 6–18 branches alternately inserted along the main axis, main axis pubescent; disarticulation above the glumes. **Spikelets** 5–12 mm long, 3–5-flowered, laterally compressed; rachilla prolonged above upper floret; callus pilose; glumes 2.8–7 mm long, the lower

usually shorter than the upper, 1-veined, the apex often mucronate; lemmas 5–7 mm long, 3-veined, the veins extending as mucros (mostly staminate plants) or into subulate awns (mostly pistillate plants), the awns 1–4 mm long, pilose on margins and each side of the midvein, apex cleft; palea as long as lemma or slightly shorter, with a narrow membranous wing on each keel (staminate plants); lodicules 2, membranous; stamens 3, anthers 2–3 mm long (staminate plants), reddish-purple; ovary glabrous, styles 2, free to base. **Caryopsis** with a fused pericarp. $2n = 24$ (Reeder, 1967).

Included taxon––*Sohnsia filifolia* (E. Fourn.) Airy Shaw (1965) [syn. *Calamochloa filifolia* E. Fourn. (1877), nom. illeg. hom. for *Calamochloë* Rchb. (1828); *Eufornia filifolia* (E. Fourn.) Reeder (1967)].

Habitat—Calcareous, rocky slopes usually on north- or east-facing slopes associated with thorn-scrub vegetation with *Muhlenbergia, Bouteloua, Erioneuron, Aristida, Eragrostis*, *Quercus, Rhus, Croton, Mimosa, Dalea, Salvia, Tagetes, Agave, Yucca, Stevia,* and *Allium*; 1100–2100 m.

Distribution—Known only from the two Mexican states: Querétaro (municipios Arroyo Seco, Cadereyta de Montes, Ezequiel Montes, Peñamiller, and Toliman) and San Luis Potosí (Municipio Guadalcázar).

Comments—Fournier (1877) originally described the genus *Calamochloa* as containing a single species, *C. filifolia*. Airy Shaw (1965) transferred the species to a new genus, *Sohnsia*, because it is confusingly similar, differing by only a single letter to *Calamochloë,* an earlier homonym (Article 53.3, ex. 14 of the International Code of Botanical Nomenclature; McNeill et al. 2006). The 3-awned nature of the lemma in *Sohnsia* is also found in the Boutelouinae, Scleropogoninae, and the Triraphideae (Peterson et al. 1997, 2016). Hitchcock (1913) did not include *Sohnsia* in his Mexican grasses simply because no material was available at this time to study in the US National Herbarium. Although, Hubbard (1934) and Sohns (1956) had aligned *Sohnsia* with the tribe Pappophoreae, now subtribe Pappophorinae in the Cynodonteae (Peterson et al. 2016). Reeder (1967) found meiotic irregularities, such as formation of 10 bivalents and four univalents at diakinesis and suggested a basic chromosome number of 10, a common number for the tribe. *Sohnsia filifolia* was collected by PMP west of Guadalcázar in 1991 [*Peterson & Annable 11129* (US)], 2010 [*Peterson, Saarela & Romaschenko 23359* (US)], and 2012 [*Peterson & Romaschenko 24675* (US)]. In 2012, only sterile specimens were found, suggesting that it does not flower every year. This may contribute to the paucity of collections for this Mexican endemic.

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REVISION OF *SPHAEROCARDAMUM* (BRASSICACEAE)

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ABSTRACT

Sphaerocardamum (Brassicaceae) is a little known and rarely collected genus that includes eight species that are endemic to limestone soils of Mexico's Chihuahuan Desert and adjacent mountain regions. In the present study species boundaries were evaluated using data from morphology, crossing experiments, cytology, genome size, and AFLP-based molecular variation. Considering variation observed from herbarium accessions and individuals cultivated in a common environment, fixed morphological character state differences support the current circumscription of *S. compressum* and *S. nesliiforme*. However, no fixed morphological states were consistent with the segregation of *Sphaerocardamum macropetalum* from *S. divaricatum* or *S. fruticulosum*, *S. macrum*, and *S. ramosum* from *S. stellatum*. Genome size variation partitioned the genome into two groups of taxa that are consistent with morphological variation and results from AFLP data are also consistent with the morphologically based groupings. In light of the available data, a taxonomic revision is presented recognizing four species: *S. compressum, S. divaricatum, S. nesliiforme,* and *S. stellatum.*

The genus *Sphaerocardamum* S. Schauer comprises eight species of Brassicaceae (Rollins 1984) native to north-central Mexico. It includes perennial or biennial herbs that typically flower from May through October following seasonal precipitation. The genus can be identified based on a combination of morphological characteristics including a caulescent diminutive habit, woody caudex, simple oblong leaves, indument of single-celled dendritically branched trichomes, white linear to spatulate petals, pale to purplish anthers, and small silicular fruits with two to eight ovules per locule (Rollins 1984; Bailey et al. 2002) (Fig. 1).

Members of the genus were primarily known from the Chihuahuan Desert and surrounding mountains in Aguascalientes, Coahuila, Hidalgo, Nuevo León, San Luis Potosí, Tamaulipas, and Zacatecas. More recent collections expand that distribution to as far to the south as Puebla and as far west as Guerrero. Populations typically occur in seasonally dry habitats on limestone soils at elevations ranging from 1560-2850 m.

In Rollins's (1941, 1984) treatments of *Sphaerocardamum*, he discussed the tentative nature of his circumscriptions because of the paucity of available material. From just 42 known sheets of *Sphaerocardamum*, he concluded that the variation could be segregated into eight putative species. The majority of the collections were designated as two widespread taxa, *S. macropetalum* Rollins and *S. stellatum* (S. Wats.) Rollins, whereas *S. compressum* (Rollins) Rollins and *S. ramosum* Rollins were known only from the type collections and the remaining species from fewer than five collections each.

The present study focuses on advancing our understanding of the taxonomy of *Sphaerocardamum* through an investigation of morphology, chromosome number, genome size, crossing studies, and amplified fragment length polymorphism data (AFLP).
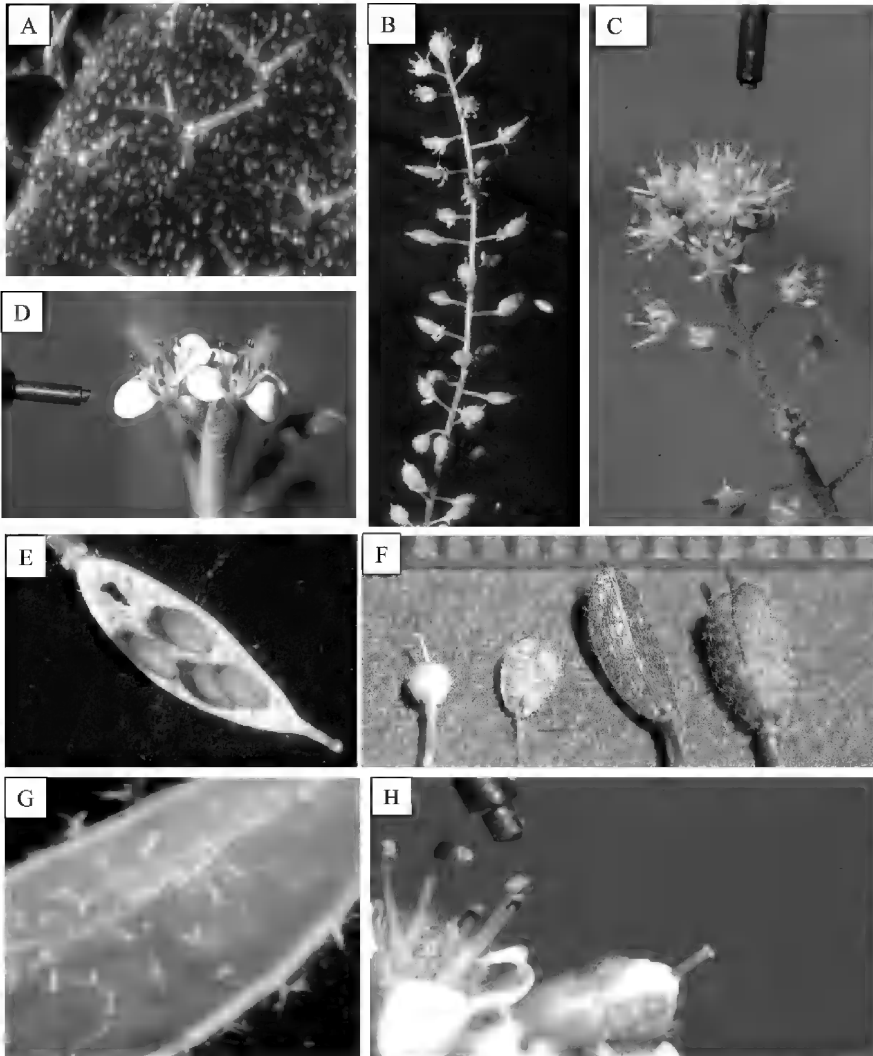
Figure 1. General morphology of *Sphaerocardamum*. A) Dendritically branched tricomes. B) Infructescence. C) *Sphaerocardamum neseliiforme* inflorescence (Bailey 157 [BH & MEXU]). D) *Sphaerocardamum macropetalum* inflorescence (*Bailey 45*). E) Replum funiculi and seeds (Bailey 57), seeds are 1 mm long. F) Siliques shape variation, left to right: *S. nesliiforme, S. stellatum, S. compressum,* and *S. macropetalum.* G) Interior fruit valve indument (Bailey 57). H) Protogyny and style morphology (Bailey 45). Scales are either a 1mm rule or the tip of a 0.5 mm diameter mechandical pencil tip. Vouchers noted are with BH and MEXU.

MATERIALS AND METHODS

Sampling. Specimens of *Sphaerocardamum* from AA, ANSM, BH, BM, ENCB, GH, JEPS, K, LL, MEXU, MO, TEX, and US herbaria were examined. New field collections were made in 1996 and 1997 (deposited in BH and MEXU). Fieldwork provided new herbarium samples as well as materials for DNA isolation, morphological studies, and seed for greenhouse-studies. Because of the limited available material, new collections from previously identified sites in addition to areas linking known localities were sought to evaluate the potential for clinal variation between the currently recognized species and/or new combinations of character states consistent with previously uncharacterized taxa. Initial comparisons of morphological variation indicated that the range of morphologies described by Rollins (1984) represented the maximum array of variation for the group (i.e., clinal variation was observed between populations but no new combination of variation were discovered). Therefore, Rollins's species limits were tested to determine whether the variation from the new collections supported the previous circumscription or if the observed intergradations blurred species boundaries, supporting more inclusive species. In cases where a collection showed intergradations between two of the species recognized by Rollins (1984), the collection was initially assigned to the species that it shared greatest geographic and morphological similarity.

Variation from all individual herbarium sheets and greenhouse grown individuals was accounted for in the morphological studies. The other sources of data (crossing studies, cytology, genome size, and AFLPs) incorporated a limited selection of the individuals (listed in subsequent sections). Because of the discrepancy of sampling and the desire to generate useful classifications, the morphologically defined species are referred to throughout and the support for those species provided by other data sources discussed within that context.

Morphology. Morphological features were compared within and between species to evaluate fixed differences between populations and to identify the range of variation within the genus. Observations were taken from herbarium sheets, 70% ethanol-pickled field collections, and live greenhouse-grown material.

Species Delimitation. The phylogenetic species concept (PSC; sensu Nixon & Wheeler 1990) was selected as the criterion for delimitation. Application of the PSC followed the general guidelines of population aggregation analysis (PAA) (Davis & Manos 1991; Davis & Nixon 1992). Those individuals sampled from a population were considered to represent the diversity of that population. Populations were compared and the minimally inclusive units maintained as distinct species if fixed characters or combinations of characters (sensu Nixon & Wheeler 1990) differed between them.

Reproductive Biology. The majority of the newly collected samples were not observed to be in flower at the time of collection. Therefore, observations and experiments regarding reproductive biology and crossing were made on plants grown from seed in the greenhouse. Artificial pollination experiments were carried out by taking anthers from the pollen donor and applying them to the stigmas of emasculated and bagged (to exclude pollinators) maternal flowers.

Cytology and Genome Size. Meiotic counts were taken from pollens mother cells (PMC) squashed from intact anther sacs of fresh greenhouse-grown material using the formic, lactic, proprionic acid-orcein stain of Jackson (1973). Flow cytometry was used to corroborate ploidy estimates for additional accessions and to estimate genome sizes. Leaf tissue of greenhouse-grown samples was analyzed on a FACS Caliber flow cytometer (Becton Dickinson, San Jose, CA) using the citric acid buffer protocol of Otto (1990) modified by Dolezel and Göhde (1995). Following the recommendation of Dolozel (pers. comm.), the centrifugation and resuspension steps were skipped and nuclei were stained using a propidium iodide plus RNase solution. Internal size standards involved the combined use of *Brassica oleracea* subsp. *acephela* (kale) and *A. thaliana.* Kale was

selected as the primary standard and run with each *Sphaerocardamum* sample because it was easy to obtain large numbers of nuclei from a single plant and its genome size did not overlap and obscure resolution of size estimates in *Sphaerocardamum*. However, that genome is slightly more than double those of *Arabidopsis* and the similar sized *Sphaerocardamum*. Therefore, the kale genome size for our sample was established via an *A. thaliana* (0.30 pg/2C for *A. thaliana* (Arumuganathan & Earle 1991)) internal standard. The single kale plant used as a standard was calculated at 1.097 pg/2C (relative to *Arabidopsis*) and used in all subsequent analysis of *Sphaerocardamum* samples.

AFLP Data. DNA extraction and purification followed Bailey et al. (2002). AFLP Small Genome Kits were purchased from ABI (Applied Biosystems, Foster City, CA) and the amplification procedure adopted followed the manufactures protocol. Primer pairs EcoRI-AC/MseI-CTA, EcoRI-AG/MseI-CTA/, EcoRI-AT/MseI-CTA, and EcoRI-AA/MseI-CTA were initially screened prior to final primer selection. Primer combinations EcoRI-AC/MseI-CTA and EcoRI-AT/MseI-CTA were selected for the final amplification because of the reproducibly amplified polymorphic markers generated across accessions. Selective amplification reactions were run on an ABI 3100 (Genetics Testing Laboratory, NMSU, Las Cruces, NM) with the GeneScan Rox 500 internal standard. GeneScan (Applied Biosystems Inc.) was used to extract peaks between 75-500 bp for each sample. GeneScan project files were imported into GenoTyper (Applied Biosystems Inc.) to establish loci and score each individual in the final matrix. A locus bin was established for any peak at least 250 units in height. Overlapping loci (bins) were excluded from the final analysis. Tables were exported to Excel for editing and peak verification using GeneScan. Polymorphic loci were imported into MVSP (Kovach Computing Systems) and UPGMA cluster analyses were obtained using the Jaccard's Coefficient. In addition, Parsimony heuristics (1000 replicates holding 10,000 trees total and 10 trees per replicate) and bootstrap analyses (1000 replicates with up to 10 trees held per replicate) were run via WinClada (Nixon 2002) in Nona (Goloboff 2000).

<div align="center">RESULTS</div>

Growth Habit. Field-collected *Sphaerocardamum* are mostly upright and 4-45 cm tall (Fig. 2A). Plants often topple over toward the end of the growing season and sometimes die back to the woody portion of the stem, which remains horizontal. Such stems can end up forming a 1-10 cm long rhizome-like structure from which upright shoots for subsequent season's growth originate. Although field-collected plants were typically upright, greenhouse-grown representatives of *S. divaricatum* and *S. macropetalum* sometimes showed a loosely decumbent habit.

The majority of greenhouse accessions began flowering within two to four months of germination. Following heavy fruitset, lateral branches from axillary buds basal to the inflorescence often form. These generally form small rosette-like structures that can apparently remain dormant for prolonged periods. During a secondary growth phase, these lateral branches become elongate stems.

Trichomes. All individuals have a moderate to dense indument of translucent dendritically branched single-celled eglandular trichomes (Fig. 1A) distributed over nearly all above-ground portions of the plant. Trichomes were never found on adaxial surface of the sepals or anywhere on petals, stamens, styles, or stigmas. Trichomes on the stem ranged from 0.05-0.8 mm tall. Occasionally (*Rollins 83347* [ENCB, GH]; *Moore 4253a* [GH]) larger trichomes (particularly on the exterior of fruit valves) appeared to have greenish spots, presumably due to the presence of chloroplasts. The relative number of ramifications of trichomes on the adaxial surface of upper cauline leaves were compared to determine whether species-specific distinctions might exist. Results from these measurements did not reveal differentiation into non-overlapping ranges (Fig. 2B). *Sphaerocardamum compressum, S. divaricatum*, and *S. macropetalum* showed greater average degrees of trichome branching than the other species, but each shared moderate overlap with some or all of the other taxa.
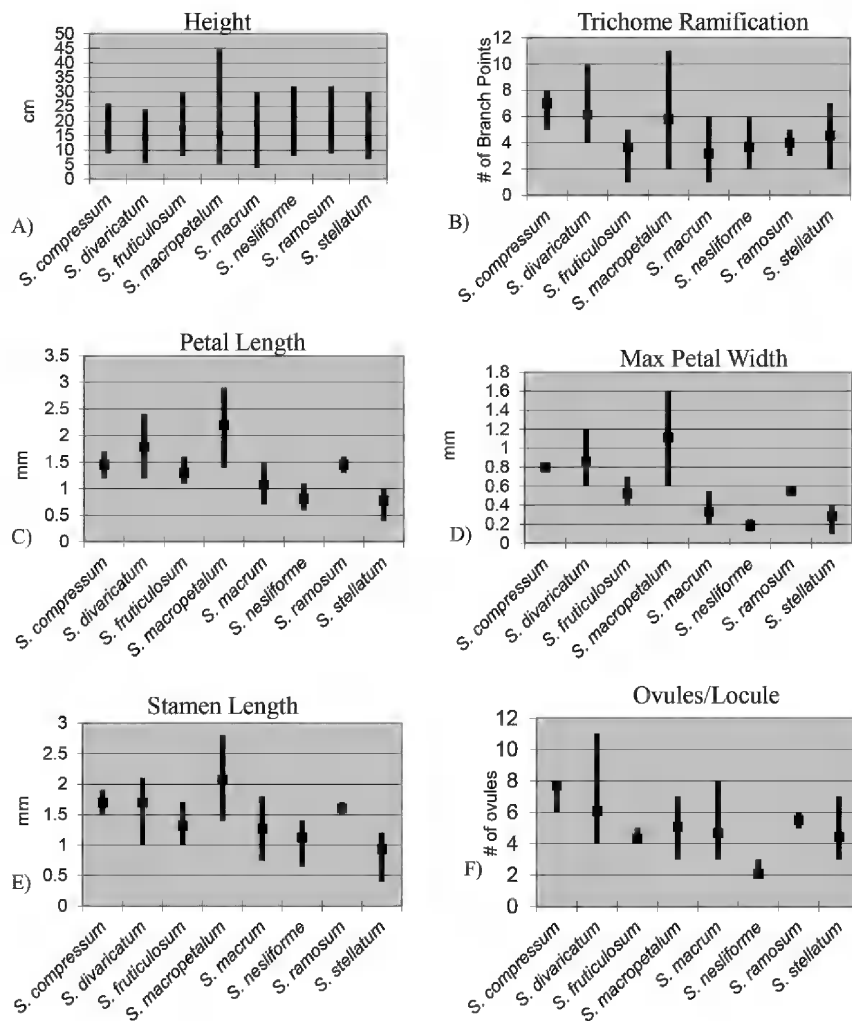
Figure 2. Morphological comparisons.
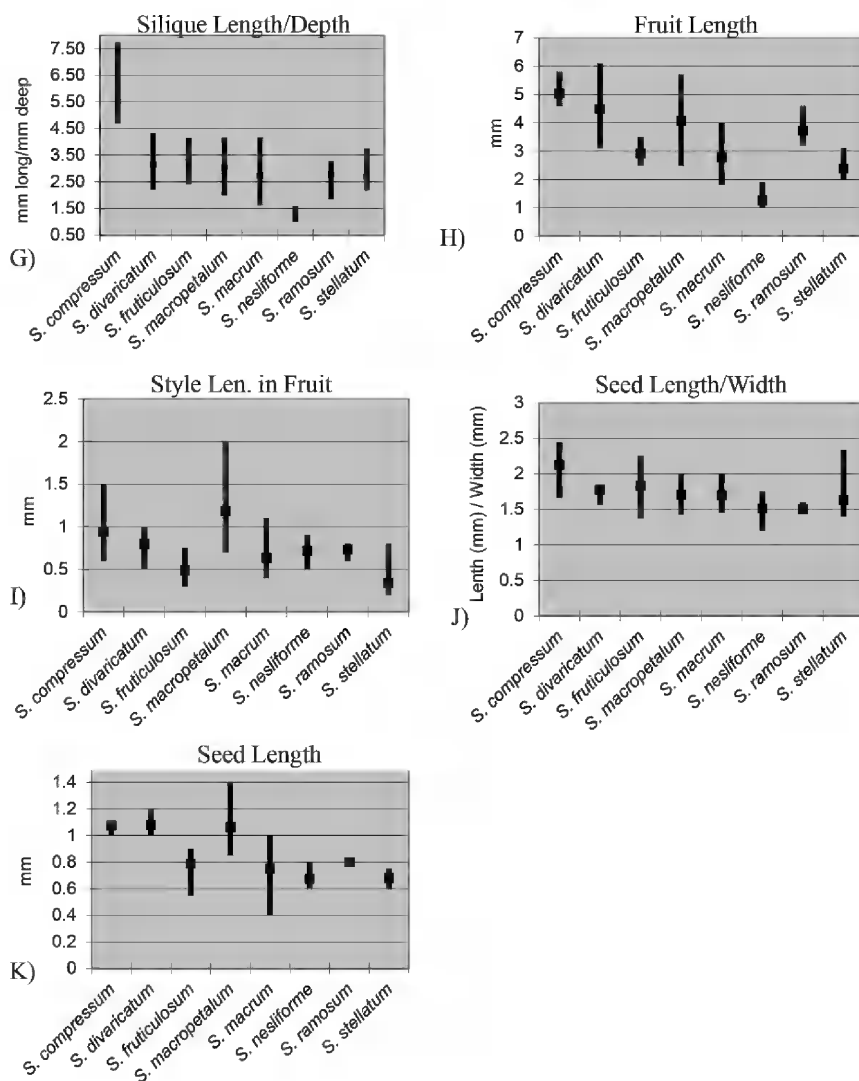
Figure 2 continued. Morphological comparisons.

Leaves. Field-collected plants were compared to identify the range of variation from natural populations. Leaf sizes ranged from 0.2-6 cm long by 0.1-1.2 cm wide, with leaves becoming progressively smaller distally. Considerable overlap in sizes and shapes were not consistent with differences between previously recognized species.

Inflorescences. The inflorescences are upright ebracteate corymbose racemes (Fig. 1B & C), which vary from simple, in some *Sphaerocardamum compressum* accessions, to paniculate in other *S. compressum* and individuals of all other *Sphaerocardamum* collections. Fruiting pedicels are straight, divaricately ascending to slightly descending, and pubescent.

Corolla. Contrary to Rollins's (1984) observations of herbarium material and a few cultivated accessions, my field and greenhouse observations did not uncover any apetalous individuals. Greenhouse observations suggest that plants pass through stages of rapid growth followed by quiescence. Quiescence follows an extended period of flowering and fruiting, and as plants become dormant they produce partially developed buds. This suggests that collections without petals may represent plants passing into a dormant phase rather than potentially apetalous species. Observations from new collections failed to identify unique differences in petal shapes and sizes between Rollins's (1984) species. These features vary both within and between species. In general, *Sphaerocardamum compressum*, *S. divaricatum,* and *S. macropetalum* have the largest petals and greatest degree of expansion from claw into a pronounced blade (Fig. 2C & D). *Sphaerocardamum macrum*, *S. nesliiforme,* and *S. stellatum* have the smallest and narrowest petals with little or no expansion.

Androecium. The subequal nature of stamens (Rollins 1984) was maintained (Fig. 1D) in greenhouse-grown accessions. Measurements from the long stamen sets ranged from ca. 0.4-2.8 mm and were exerted beyond the perianth in all collections. *Sphaerocardamum compressum, S. divaricatum, S. macropetalum,* and *S. ramosum* have the greatest average stamen lengths, but there is considerable overlap between previously recognized species (Fig. 2E).

Pollen. Pollen grains were mounted in glycerin and observed using light microscopy at 400X. All observed pollen grains conformed to the typical tricolpate Brassicaceae type, and they ranged from 27-30 µm long by 13-16 µm wide. No taxonomically informative characters were observed with respect to gross pollen morphology or size.

Gynoecium. The vast majority of collections displayed 2-8 ovules per locule (Fig. 2F), with a single collection of *Sphaerocardamum divaricatum* containing 10-11 ovules per locule (*Rzedowski 6551*[TEX]). *Sphaerocardamum nesliiforme* accessions contained two ovules per locule, with an occasional individual fruit having a third ovule (e.g., *Moore 5443* [GH]; *Bailey & Ochoterena 157* [BH, MEXU]). The other species range from four to eight ovules (occasional individual fruits with 3-9 ovules).

Fruit shape varies from spherical in *Sphaerocardamum nesliiforme,* to oblong in *S. compressum*, *S. divaricatum,* and *S. macropetalum*, to obovate in *S. fruticulosum, S. macrum, S. ramosum,* and *S. stellatum* (Fig. 1F). Fruits can be uncompressed or compressed perpendicular to the septum. An estimation of compression relative to length was made to quantify the degree of compression (fruit length/depth ratio; Fig. 2G). Values greater than one identify angustiseptate-compressed fruits, whereas values closer to one identify relatively uncompressed spherical fruits. Estimates for *S. compressum* and *S. nesliiforme* revealed differentiable variation in silicle shape with greatest and least compression respectively. The remaining species share similar averages and ranges with respect to

Overall fruit size was estimated by length (Fig. 2H). *Sphaerocardamum nesliiforme* has the smallest fruits while *S. compressum, S. divaricatum,* and *S. macropetalum* have the largest fruits.

Considerable overlap exists between species with respect to fruit length except for *S. nesliiforme,* which rarely produces fruits that are long enough to overlap with variation from *S. macrum*.

Table 1. Interspecific crosses. The first four columns identify the species and accession of the maternal parent and paternal parent, respectively. The number of presumably viable (normal shape and size) seeds recovered from each fruit are provided in the fifth column. Note: not all crosses were attempted and crosses not included should not be considered unsuccessful. "*" – with the paternal donor cross indicates that F1 seed were grown to maturity. "1" - self-pollinated accessions producing seed.

Maternal Parent		Paternal Parent		
Species	Accession	Species	Accession	Seeds
S. divaricatum[1]	158	*S. fruticulosum*	142	0
	158	*S. macropetalum*	137	0
	158	*S. macrum**	57	4
	158	*S. macrum*	126	0
	158	*S. ramosum**	125	3
	158	*S. ramosum*	125	2
	158	*S. nesliiforme*	157	3
S. fruticulosum[1]	144	*S. fruticulosum*	141	6
	144	*S. divaricatum**	93	7
	144	*S. nesliiforme*	157	0
S. macropetalum[1]	137	*S. fruticulosum*	144	1
	137	*S. macrum*	122	3
	137	*S. macrum**	128	3
	137	*S. ramosum**	125	4
S. macrum[1]	128	*S. divaricatum*	158	4
	128	*S. fruticulosum*	141	2
	128	*S. fruticulosum**	142	5
	57	*S. fruticulosum**	141	10
	57	*S. macropetalum**	93	2
	128	*S. divaricatum**	93	5
	128	*S. macrum*	57	1
	128	*S. macrum*	57	8
	128	*S. nesliiforme**	152	8
	57	*S. nesliiforme**	157	2
	128	*S. nesliiforme**	157	8
	128	*S. ramosum**	125	6
S. nesliiforme[1]	157	*S. fruticulosum*	141	3
	152	*S. fruticulosum**	142	4
	152	*S. macropetalum**	137	2
	157	*S. macrum*	57	4
	152	*S. ramosum*	125	2

Interior Valve Indument. Trichomes on the interior of fruit valves are relatively uncommon within Brassicaceae. Aside from *Sphaerocardamum compressum, Sphaerocardamum* species all display a sparse to dense indument on the interior surface of the fruit valves (Fig. 1G). These trichomes are mostly dendritic, but often less ramified than the exterior valve trichomes on the same fruit. In a few cases (e.g., *Purpus 5235* [UC], *5374* [US]; *Wells & Nesom 99* [GH]), they show reduction to malpighiaceous or minute, apparently simple, forms. All observed valves of *S. divaricatum, S. macropetalum, S. macrum, S. nesliiforme,* and *S. ramosum* accessions showed some level of interior pubescence. Individual valves on two plants of some *S. stellatum* (*Pringle 2844* [GH]; *Palmer 752* [GH, NY]) ranged from glabrous to pubescent.

Style. Previous knowledge of style lengths suggested that mature styles ranged from ca. 0.5 mm in *Sphaerocardamum stellatum* to more than 2 mm in *S. macropetalum*. Observations for the present study indentified style lengths from 0.2-2 mm (Fig. 2I). They are greatest in *S. compressum, S. divarticatum,* and *S. macropetalum* with the remaining species overlapping with the lower range for these two long-styled species.

Seed. All observed individuals had incumbent cotyledons. Seed shape was estimated by length to width ratio (Fig. 2J). This estimate supports strong similarity in overall seed shape within and between species. Relative seed size was subsequently estimated by length (Fig. 2K), which identified more variation than shape. *Sphaerocardamum compressum, S. divaricatum,* and *S. macropetalum* have the largest seeds, whereas the five other species have smaller seeds. Although there is variation in seed length, there is also considerable overlap in ranges. Seeds were viable for extended periods, with field-collected seed successfully germinated up to three years after collection following storage in paper envelops at room temperature and humidity. However, a recheck of seeds stored under these conditions after five years recovered very low seed viability, highlighting the need to store these seeds under more optimal conditions.

Reproductive Biology. Protogyny was illustrated by stigmas protruding from the closed buds in greenhouse grown *Sphaerocardamum divaricatum, S. fruticulosum, S. macropetalum, S. macrum,* and *S. nesliiforme* (Fig. 1H). Protogyny appeared was common in the early stages of flowering, with flowers/buds initiated later in the cycle rarely displaying the trait. *Sphaerocardamum stellatum* and *S. ramosum* often appeared to have fully developed stigmas well before the anther sacs matured and dehisced, suggesting additional cases of functional protogyny. No observations were made for *S. compressum,* because accessions rarely flowered in the greenhouse, and those that did finished flowering before protogyny in the genus was noted. Stamens were generally spreading at anthesis, but commonly flex inward, coming into contact with the style or stigma late in flower development. This was most frequently observed in the shorter-styled accessions. However, the timing of style elongation appeared to be variable in the longer-styled accessions and some long-styled accessions were observed with anthers touching the stigma prior to full elongation.

The shorter-styled species generally produced seed when bagged to exclude pollinators, suggesting that they are self-compatible and selfing under some conditions. The longer-styled species, *Sphaerocardamum divaricatum, S. macropetalum*, and *S. nesliiforme,* had to be intentionally self-pollinated to produce self seed. Seed set among field-collected individuals was noticeably higher than in cultivated accessions.

Artificial crosses were made as a measure of potential reproductive isolation. Individuals grown from accessions collected from populations used in Rollin's (1984) treatment were used in the crossing studies. Table 1 lists each cross and the resulting seed per fruit (abnormal seed morphologies were not observed). Because these experiments were dependent on accessions flowering simultaneously in the greenhouse, not all crosses were possible. However, given the results available, it appears that all of these populations, representing seven of eight of Rollins's species, can be

crossed. Although a few crosses failed to produce seed, these single attempts do not particularly support a conclusion of reproductive isolation. For all failed cases, alternative crosses involving the same species pairs were successful. Therefore, the unsuccessful crosses may have been due to poor timing or growth conditions during pollination and fruit development. Germination of F1 seed for a subset of crosses were all successful, but F1 fertility was not measured. Furthermore, a cross involving *Sphaerocardamum ramosum* (125) pollen and a *Halimolobos minutiflora* (145B; a diploid *Halimolobos* accession; Bailey unpubl.) stigma produced plump viable-looking seeds, suggesting that intergeneric crosses are also possible.

Chromosome number. Previous cytological studies of *Sphaerocardamum* were limited to three observations of $n = 8$ (a single accession of *S. macropetalum* and two accessions of *S. stellatum* (Rollins and Rüdenberg 1971, 1977)). Table 2 lists haploid chromosome numbers observed in this study. Counts for *Sphaerocardamum* ranged from $n = 7–9$, with the majority considered $n = 8$. Photographs of representative meiotic squashes are provided in Fig. 3.

Table 2. Haploid chromosome counts.

Taxon	Voucher	squash date	$n =$
S. compressum	115	6 Dec '99	8
S. divaricatum	158	19 Nov '98	8
S. fruticulosum	142	19 Aug '99	8
S. fruticulosum	144	4 July '98	8
S. macropetalum	45	15 Oct '98	7 & 8
S. macropetalum	45	19 Aug '99	8
S. macropetalum	137	19 Nov '98	8
S. macropetalum*	—	—	8
S. macrum	128	15 Oct '98	8
S. nesliiforme	157	15 Oct '98	8
S. ramosum	125	19 Nov '98	8 & 9
S. ramosum	125	19 Nov '98	8
S. stellatum	122	5 Nov '98	7-8
S. stellatum*	—	—	8

Note: counts followed by a "*" are from Rollins and Rudenberg (1977, 1979). A "–" indicates that a clear distinction could not be made, whereas an "&" notes that two distinct numbers were clearly identified.

Flow cytometry. Genome sizes from greenhouse grown samples ranged from 0.29-0.36 pg/2C (Table 3). The genomes of these species can be divided into two size classes (two tailed unpaired t-test, p-value 0.00005): 1) 0.340-0.360 pg/2C for *Sphaerocardamum compressum, S. divaricatum*, and *S. macropetalum* genomes; and 2) 0.294-0.325 pg/2C for *S. fruticulosum, S. macrum, S. nesliiforme, S. ramosum*, and *S. stellatum* (Fig. 4). Plants grown from F1 seed of greenhouse crosses between taxa with different genome sizes almost all displayed genome sizes intermediate between their parental types (Table 3). The one exception was the 128 x 152 cross, which displayed a larger genome size than either parent.

AFLP. AFLP runs resulted in the identification of 89 variable non-overlapping loci from 21 accessions (Table 4). Both UPGMA clustering (Fig. 5A) and parsimony analysis (Fig. 5B) clearly resolved representatives of *Sphaerocardamum compressum* and *S. nesliiforme* as distinct lineages within the genus. *Sphaerocardamum divarticatum* and *S. macropetalum* accessions resolved within a single mixed group/clade. In the parsimony analysis *S. fruticulosum, S. macrum, S. ramosum*, and *S stellatum* accessions resolved within a single mixed clade with low support and in the UPGMA dendrogram these taxa form a grade leading to *S. nesliiforme*.

Table 3. DNA Content. Vouchers replicated in two or more rows signify individuals measured on different days or, if they are followed by ∎ superscript, different individuals from the same population.

Taxon	Voucher	pg/2C
S. compressum	104	0.347
	104	0.348
	115	0.354
S. divaricatum	158	0.340
	93	0.344
	99	0.348
S. fruticulosum	142	0.319
S. macropetalum	45	0.359
	137	0.341
S. macrum	57	0.316
	122	0.326
	126	0.305
	128	0.309
	132	0.315
S. nesliiforme	152	0.306
	156	0.321
	157	0.319
S. ramosum	125 [1]	0.304
	125 [1]	0.294
	125 [2]	0.311
S. stellatum	120	0.306
hybrid	137x125	0.315
hybrid	158x125	0.317
hybrid	57x93	0.327
hybrid	157x141	0.318
hybrid	128x152	0.316

Table 4. Molecular sampling and voucher Information.

Taxon	Collection/Herbarium
Sphaerocardamum compressum (Rollins) Rollins	Bailey & Ochoterena 104 / BH & MEXU
Sphaerocardamum compressum (Rollins) Rollins	Bailey & Ochoterena 115 / BH & MEXU
Sphaerocardamum divaricatum (Rollins) Rollins	Bailey & Ochoterena 99 / BH & MEXU
Sphaerocardamum divaricatum (Rollins) Rollins	Bailey & Ochoterena 158 / BH & MEXU
Sphaerocardamum fruticulosum (Rollins) Rollins	Bailey & Ochoterena 142 / BH & MEXU
Sphaerocardamum fruticulosum (Rollins) Rollins	Bailey & Ochoterena 144 / BH & MEXU
Sphaerocardamum macropetalum (Rollins) Rollins	Bailey 15 / BH & MEXU
Sphaerocardamum macropetalum (Rollins) Rollins	Bailey 45 / BH & MEXU
Sphaerocardamum macropetalum (Rollins) Rollins	Bailey 47 / BH & MEXU
Sphaerocardamum macropetalum (Rollins) Rollins	Bailey & Ochoterena 133 / BH & MEXU
Sphaerocardamum macropetalum (Rollins) Rollins	Bailey & Ochoterena 137 / BH & MEXU
Sphaerocardamum macrum (Standley) Rollins	Bailey 57 / BH & MEXU
Sphaerocardamum macrum (Standley) Rollins	Bailey & Ochoterena 126 / BH & MEXU
Sphaerocardamum macrum (Standley) Rollins	Bailey & Ochoterena 128 / BH & MEXU
Sphaerocardamum macrum (Standley) Rollins	Bailey & Ochoterena 132 / BH & MEXU
Sphaerocardamum macrum (Standley) Rollins	Bailey & Ochoterena 131 / BH & MEXU
Sphaerocardamum nesliiforme Schauer	Bailey & Ochoterena 152 / BH & MEXU
Sphaerocardamum nesliiforme Schauer	Bailey & Ochoterena 156 / BH & MEXU
Sphaerocardamum nesliiforme Schauer	Bailey & Ochoterena 157 / BH & MEXU
Sphaerocardamum ramosum Rollins	Bailey & Ochoterena 125 / BH & MEXU
Sphaerocardamum stellatum (S. Wats.) Rollins	Bailey & Ochoterena 120 / BH & MEXU

Note: Accessions in bold face type were used in Bailey and Doyle (1999).

DISCUSSION

The culmination of data from all available collections, including the 42 available to Rollins (1984) and 75 new samples, eliminated previously discrete boundaries between morphological features used to distinguish several species of *Sphaerocardamum*. Furthermore, the study of morphology did not identify any new characters or character combinations that would suggest the existence of previously uncharacterized species. Since the morphological data were recorded from all available collections, while all other studies involved subsampling accessions, I focus the initial evaluation of species boundaries on the morphological findings and then discuss whether the other relevant data sources support, refute, or provide no useful information in comparison to conclusions based on morphology.

The distinctiveness of accessions representing *Sphaerocardamum compressum,* relative to other species, was supported by the complete absence of trichomes on the interior of fruit valves and

by the fruit length to width ratio (Fig. 2G). Fruits of *S. compressum* are among the longest and are the widest, resulting in a highly compressed angustiseptate form with a greater than average number of ovules per ovary (Fig. 2F). These features were maintained in greenhouse-grown accessions and these individuals differed from accessions of other species by remaining largely unbranched and rarely flowering in cultivation. This group of accessions is clearly most similar to those representing *S. divaricatum* and *S. macropetalum*, which are also robust plants with relatively large petals and fruits, shared nuclear DNA content (Fig. 4), and greater ramification of leaf trichome branching (Fig. 2B). However, in addition to differing in the key traits noted above, *S. compressum* was supported as a distinct cluster and clade the UPGMA and parsimony trees (Fig. 5), respectively.

An assessment of morphology, geography, genome size, crossing data and AFLP data all failed to clearly differentiate accessions of *Sphaerocardamum divaricatum* and *S. macropetalum*. These accessions are distinct from *S. compressum* (noted above), but share overlap in essentially all other features. In general, it seems those individuals previously assigned to *S. divaricatum* display somewhat smaller flowers overall (petals, stamens, and style length), larger fruits, and shorter styles, but none of these are strikingly different. Furthermore, accession representing the geography of these two species were intermixed in the AFLP analysis (Fig. 5).
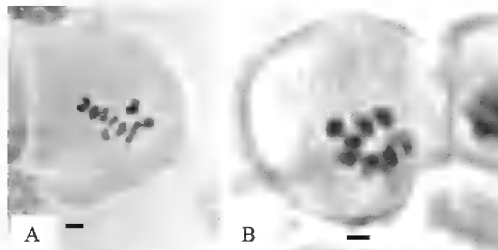
Figure 3. Representative meiotic chromosome counts. Oil immersion at 1000x (scales = 5 μm). A) *S. macropetalum*, n = 8 (Bailey & Ochoterena 45 [BH & MEXU]. B) *S. fruticulosum*, n = 8 (Bailey & Ochoterena 142 [BH & MEXU]).
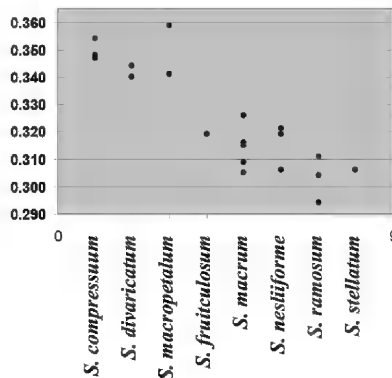
Figure 4. Genomic DNA content in picograms per diploid genome (pg/2C).
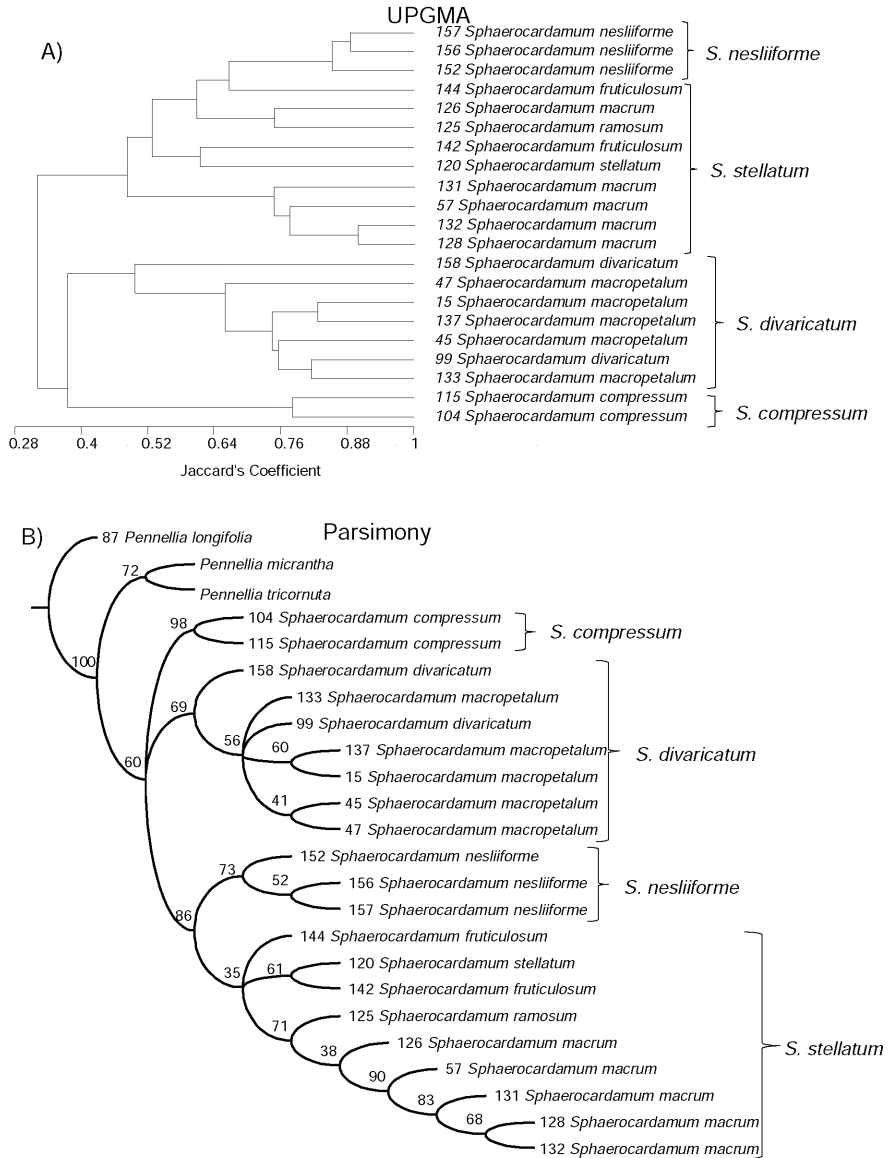
Figure 5. Analysis of AFLP data. A) UPGMA dendrogram derived from clustering using Jaccard's coefficient. B) Parsimony derived strict consensus tree with bootstrap percentages from 1000 replicates. Species names at the tips of branches represent *a priori* assignments and species names summarizing groups represent the species recognized herein.

Like *Sphaerocardamum compressum,* populations of *S. nesliiforme* were distinctive relative to all other species. They all displayed two ovules per locule with a very few individual plants displaying a third ovule in a couple of locules observed (Fig. 2F). This is in contrast to all other species, none of which were observed to ever have two ovules per locule. In addition, the small spherical fruits differ from all other species of *Sphaerocardamum* and these features were maintained in the common garden grown accessions. Though highly distinctive, the species is most closely aligned with *S. fruticulosum, S. macrum, S. ramosum,* and *S. stellatum.* Results from the analysis of AFLP data group accessions of *S. nesliiforme* into an exclusive cluster (UPGMA, Fig 5A) and clade (parsimony, Fig. 5B)

The remaining four taxa (*Sphaerocardamum fruticulosum, S. macrum, S. ramosum,* and *S. stellatum*) also shared considerable overlap in their morphology, genome sizes, and they resolved together in the UPGMA and parsimony analyses (Fig. 5). The key features used to previously distinguish these taxa were derived from observations of few accessions and it was often impossible to apply any trait other than geography when attempting to classify newly available accessions aligned with these taxa. Ultimately this group, like *S. divaricatum* plus *S. macropetalum,* appears to represent a fairly widespread and common lineage. They are clearly distinguished from the aforementioned groups by relatively short oblong (not spherical) fruits (Fig. 1F), short linear petals (Fig. 2D), and relatively short seeds (Fig. 2K). They also resolved as a weakly supported clade in the parsimony analysis (Fig. 5B) and as a grade of individuals in the UPGMA clustering (Fig 5A).

While it was hoped that chromosome and crossing data would identify additional features to differentiate these individuals and populations into putative species-level lineages, neither provided much in the way of variable characters. Lack of variability can be consistent with accessions that all represent single taxa, but when compared to other features that are fixed between populations these are interpreted as ancestral features that have simply not diverged in these cases (e.g., Rosen 1979), providing essentially no information to refute species limits relative to other characters that do show variability among populations.

TAXONOMIC HISTORY AND TREATMENT

The relatively short (1847-present) and convoluted taxonomic history of *Sphaerocardamum* is exemplified by the historical assignment of its species to four different genera (*Capsella* Medik., *Cibotarium* O.E. Schulz, *Lepidium* L., and *Sphaerocardamum*) and multiple Brassicaceae tribes. The type for the genus, *Sphaerocardamum nesliaeforme,* was described in 1847 by Sebastian Schauer to accommodate a specimen collected by Alwin Aschenborn from central Mexico. Sereno Watson described *Capsella stellata* in 1890 from Carneros Pass (Coahuila) collections of C. G. Pringle. The preeminent German cruciferologist O.E. Schulz, who wrote the Cruciferae treatment for Engler and Prantl's *Die Natürlichen Planzenfamilien,* erected *Cibotarium* in 1933 to accommodate *C. stellata.* A few years later, Standley (1937) described *Lepidium macrum* from Nuevo León collections of C.H. Mueller. About the same time, R.C. Rollins, who became the premier North American Cruciferae systematist of his time (see Al-Shehbaz 1999), began addressing the group as a side project to his dissertation research on *Arabis.* Rollins had collections for all the aforementioned species except the type of the monotypic *Sphaerocardamum,* which was housed in the Berlin herbarium and unavailable to Rollins during World War II. Rollins recognized the affinities between *Cibotarium stellatum, Lepidium macrum* and several newer collections available at the Gray Herbarium and concluded that these all belonged to *Cibotarium.* He subsequently transferred *L. macrum* and described *C. divaricatum, C. divaricatum* var. *compressum, C. fruticulosum,* and *C. macropetalum* (Rollins 1941). In that treatment, members of *Cibotarium* were united and considered distinct from *Capsella* and *Lepidium* based on their exerted purplish anthers, three to eight ovules per locule, and nearly equal stamen lengths. Aside from Rollins's (1957) description of *C. microcarpum,* from a Hidalgo collection of H.E. Moore, no additions or changes were made to the genus until the early 1980's.

Forty years after Rollins revised *Cibotarium*, he had the opportunity to view the type material of *Sphaerocardamum nesliaeforme* for the first time. Comparison of this collection to members of *Cibotarium* were sufficient to recognize *C. microcarpum* was synonymous with *S. nesliaeforme*. Rollins concluded that Schulz had incorrectly erected *Cibotarium* for *Capsella stellata*, which Rollins decided best fit under *Sphaerocardamum*. Subsequently, Rollins abandoned *Cibotarium* in favor of *Sphaerocardamum*, which had priority. In addition, he elevated *C. divaricatum* var. *compressum* to *S. compressum,* described *S. ramosum* from a single new collection (Rollins 1984), and corrected an orthographic error in the type so that *S. nesliaeforme* has subsequently been known as *S. nesliiforme.*

In Schulz's 1936 classification, *S. nesliiforme* and species of *Arabidopsis* Heynhold, *Christolea* Camb., *Cymatocarpus* O.E. Schulz, *Drabastrum* (F.v. Mueller) O.E. Schulz, *Geococcus* J. Drummond, *Halimolobos* Tausch, *Harmsiodoxa* O.E. Schulz, *Lamphophragma* O.E. Schulz, *Lemphoria* O.E. Schulz, *Micromystria* O.E. Schulz, *Nasturtiopsis* Boiss., *Pachymitus* O.E. Schulz, *Pennellia* Nieuwl., *Pseudarbidella* O.E. Schulz, and *Scambopus* O.E. Schulz were all placed in the subtribe Arabidopsidinae of the Sisymbrieae. In contrast, the other species of *Sphaerocardamum* (known then as *Cibotarium stellata* O.E. Schulz) was assigned to subtribe Capsellinae of the Lepidieae along with *Capsella, Greggia* A. Gray, *Hartwegiella* O.E. Schulz, *Hedinia* Ostenfeld, *Hornungia* Reichenb., *Hutchinsia* R. Brown, *Hymenolobos* Nutt., *Mancoa* Weddell, *Phlegmatospermum* O.E. Schulz, and *Synthlipsis* A. Gray.

Recent phylogenetic studies based on DNA sequences and morphology have consistently resolved a well-supported *Sphaerocardamum* within a strictly New World group of Brassicaceae, the tribe Halimolobeae (Bailey & Doyle 1999; Bailey et al. 2002; Bailey et al. 2007). The latter is also well-supported within a larger "Arabidopsoid lineage" (Bailey et al. 2002) that has become known as Brassicaceae Lineage 1 (Beilstein et al. 2006; Beilstein et al. 2008). As currently recognized Halimolobeae comprise five genera (*Exhalimolobos* [9 spp.]*, Halimolobos* [8 spp.]*, Mancoa* [9 spp.]*, Pennellia* [10 spp.], and *Sphaerocardamum* [4 spp. recognized here]) that are distributed from the southwestern USA to the Andes (Price et al. 2001; Bailey et al. 2007; Hernández-Sandoval & Martínez 2013). A combination of geography and morphological features can be used to help diagnose Halimolobeae. The morphological features include branched unicellular trichomes, ebracteate racemes, white petals, mucilaginous seeds, and x = 8 base chromosome numbers (Bailey et al. 2007). Nearly all these taxa occur in remote under collected areas and therefore little is known about their overall distribution, variation, or biology.

SPHAEROCARDAMUM S. Schauer, Linnaea 20: 720. 1847. **TYPE:** *Sphaerocardamum nesliiforme* S. Schauer

Cibotarium O. E. Schulz, Engl. Jahrb. 66: 91. 1933. **TYPE:** *Cibotarium stellatum* S. Wats.

Biennial or perennial **herbs,** sometimes subshrubs, with a woody caudex, 5-40 cm tall, plants often dying back to the caudex, which can form a short (≤10 cm) rhizome-like structure in subsequent seasons. **Roots** forming a taproot system without obvious adventious roots. **Trichomes** translucent (rarely greenish), unicellular, eglandular, and dichotomous dendritically branched; covering most aerial portions of the plant. **Stems** erect to ascending or decumbent, terete, simple or branched apically and/or basally, sometimes developing from adventious buds on roots, moderately to densely pubescent. **Leaves** cauline (not rosulate), petiolate to sessile, simple oblanceolate to elliptic, moderately to densely pubescent; blade margins entire to sparingly and irregularly dentate, apex and teeth terminating in a single trichome. **Peduncle** erect. **Inflorescence** a dense terminal corymbose ebracteate raceme, simple to compound. **Pedicels** divaricately ascending to slightly descending, 3-5 mm apart, straight terete, 2-6 mm long, pubescent. **Perianth** actinomorphic, 1-3 mm across. **Sepals** erect to spreading, oblong, non-saccate, hyaline-margined, 0.5-2.0 mm long, 0.3-1.0 mm wide, caducous; abaxial surface pale to purplish, sparsely to densely pubescent; adaxial surface smooth,

glabrous. **Petals** 4 (0), narrowly oblanceolate to spatulate with a claw, 0.4-2.9 mm long, 0.1-0.2 mm wide at the proximal end, 0.1-1.6 mm wide at the distal end, white; apex obtuse, glabrous; margin entire; petals occasionally absent. **Stamens** 6 (4+2), exserted, subtetradynamous; **filaments** white to translucent (sometimes with a purplish base), glabrous; **anthers** purple to pale yellow, dithecal, oblong, rounded at base, obtuse at apex, glabrous, dehiscence introrse; pollen yellow. **Gynoecium** spherical to oblong, moderately to densely pubescent; often protogynous; **styles**, 0.5-2 mm long, glabrous; **stigmas** capitate to obscurely bilobed with lobes over the septum margins, papillate; **ovules** biseriately attached 2-8 (rarely 10-11) per locule, plump. **Fruit,** spherical to oblong, uncompressed to strongly angustiseptate, 1-6 mm long, minute apical notch present or absent, pubescent, dehiscent, some fruits remaining attached for extended periods; **valves** keeled or rounded on the dorsal side, densely pubescent on the exterior, glabrous to moderately pubescent on the interior; **septum** membranaceous to scarious, complete to perforate, glabrous; **funiculi** free from the septum, glabrous. **Seeds** uniseriately to biseriately arranged, 2-8 (rarely 10-11) per locule, oblong and plump; seed coat golden to brown, reticulate, mucilaginous when wetted, glabrous; cotyledons incumbent. **Seedlings** with epigeal germination; cotyledons entire, fleshy, glabrous to sparsely pubescent.

Species of *Sphaerocardamum* are restricted to Mexico on limestone soils in arid habitats of the central and southern Chihuahuan Desert. More specifically, populations are known from a fairly contiguous swath of the region from Sierra de Parras in southern Coahuila to Hidalgo with single disjunct populations found in Puebla and Guerrero. Each locality tends to have individuals broadly spaced across the landscape, making it difficult to find more than a few of these cryptic plants. However, the rarity of species within the genus is questionable. Just a few weeks of fieldwork following a good rainy season recovered many populations, suggesting more *Sphaerocardamum* populations exist that have not been discovered because of seasonality, the remoteness of localities, and difficulty involved in spotting individuals. Furthermore, the habitat for *Sphaerocardamum* species does not appear to be under threat from significant human related disturbance. Aside from grazing, little disturbance was noted within most *Sphaerocardamum* habitats and we rarely observed evidence of grazing on *Sphaerocardamum.*

Key to *Sphaerocardamum* species

1. Silique uncompressed-globose, 1–1.5 mm in diameter, septum nearly circular; seeds two per locule (rarely a third in a few fruits); styles ca. 0.5–0.7 mm long .... **Sphaerocardamum nesliiforme**

1. Silique moderately to highly compressed perpendicular to the septum (angustiseptate – fruits wider than deep), septum elliptic to narrowly oblong; seeds 3–11 per locule; styles 0.2–2.0 mm long.

    2. Petals mostly as long as sepals, 0.1–0.7 mm wide at the distal end; siliques obovate, ca. as long as wide, 2–4.5 mm long, moderately angustiseptate; valves keeled on the back, pubescent on the interior (rarely a mixture of pubescent and glabrous valves on the same individual); apical notch at the base of the style present or absent; styles in fruit 0.2–1.1 mm long; seeds 0.4–1 mm long
    ....**Sphaerocardamum stellatum**

    2. Petals longer than sepals, 0.6–1.6 mm wide at the distal end; silique oblong, mostly twice as long as wide (or longer), 2.5–6 mm long, moderately to strongly angustiseptate; valves keeled or rounded on the back, pubescent or glabrous on the interior; apical notch mostly wanting; styles in fruit 0.5–2.0 mm; seeds 0.8–1.4 mm long.

        3. Silique weakly angustiseptate (septum length to depth ratio 1.75–4.4), septum elliptic; valves mostly rounded on back and pubescent on the interior .... **Sphaerocardamum divaricatum**

        3. Silique strongly angustiseptate (septum length to depth ratio 4.7–7.25); septum narrowly oblong; valves always keeled on back and glabrous on the interior .... **Sphaerocardamum compressum**

1. SPHAEROCARDAMUM COMPRESSUM (Rollins) Rollins, Contrib. Gray Herb. 213: 13. 1984.
Cibotarium divaricatum var. *compressum* Rollins, Contrib. Dudley Herb. 3: 180. 1941.
T**YPE**: **MEXICO. Coahuila**. Sierra De Parras, July 1910, *C.A. Purpus 4603* (holotype:
GH!; isotypes: UC!, US!). Figures. 6 & 7.

Biennial or perennial 9-26 cm tall. **Stems** erect, often unbranched, moderately to densely
pubescent. **Leaf** margins entire to denticulate, trichomes with 5-8 ramifications. **Inflorescence**
simple to compound. **Pedicels** 4-7 mm long, divaricately ascending. **Perianth** spreading. **Sepals**
1.2-1.4 mm long and 0.5-0.6 mm wide. **Petals** spatulate with distinct claw and blade, 1.2-1.7 mm
long and ca. 0.8 mm wide at the distal end. **Filaments** 1.5-1.9 mm long; **anthers** purple.
Gynoecium oblong; **ovules** 6-8 per locule. **Fruit** oblong, strongly angustiseptate, 4.6-5.8 mm long,
1.9-2.4 mm wide, 0.75-1.0 mm deep, minute apical notch mostly absent; **styles** 0.6-1.5 mm long;
stigmas capitate entire to obscurely bilobed; **valves** keeled, densely pubescent on the exterior,
glabrous on the interior. **Seeds** uniseriate to biseriate arrangement, 6-8 per locule, oblong and plump
1.0-1.1 mm long and 0.45-0.6 mm wide. $n = 8$.

Phenology. Only known to flower in July (information from the type specimen only, all
other collections lack flowers).

Sphaerocardamum compressum is easily distinguished from other *Sphaerocardamum* species
by its 6-8 seeds per locule, glabrous fruit valve interiors, and strongly angustiseptate-compressed
siliques. The majority of specimens for *S. compressum* suggest that plants are among the shortest and
least branched of *Sphaerocardamum* species. Geographically *S. compressum* is restricted to the
mountains of southern Coahuila (Fig. 7), which limits the species to the northernmost range for the
genus. Populations are only known from southern Coahuila on limestone soils of Sierra de Parras as
well as the smaller ranges to the east of Saltillo. The distribution *of S. compressum* only overlaps
slightly with the range of *S. divaricatum,* and these two species have only been collected growing in
reasonably close proximity from one locality. *Sphaerocardamum compressum* have been found at the
highest known elevations for *Sphaerocardamum*, from 2000-2900 m, with *Abies*, *Agave*,
Arctostaphylos, Dasylirion, Pinus cembroides, Pseudotsuga, Quercus, and *Spirea.*

The labels for the holotype and isotypes of *Sphaerocardamum compressum* (*Purpus 4603*)
each have a hand written "4603=1027." Purpus 1027 sheets correspond to the type of *S. divaricatum*.
The different dates and accession numbers on these presumably mean that Purpus believed that these
represented collections of the same species from different localities. The idea that these two distinct
morphological forms were not collected sympatrically is further supported by the morphology of the
specimens in each of the two sets of collections. All specimens on the 1027 sheets are
morphologically defined as *S. divaricatum*, whereas all specimens on the 4603 sheets correspond
morphologically to *S. compressum*. If Purpus had collected these from the very same locality, on
different dates, and considered them the same species, one would expect that a mixture of
morphological forms would be found in the two sets
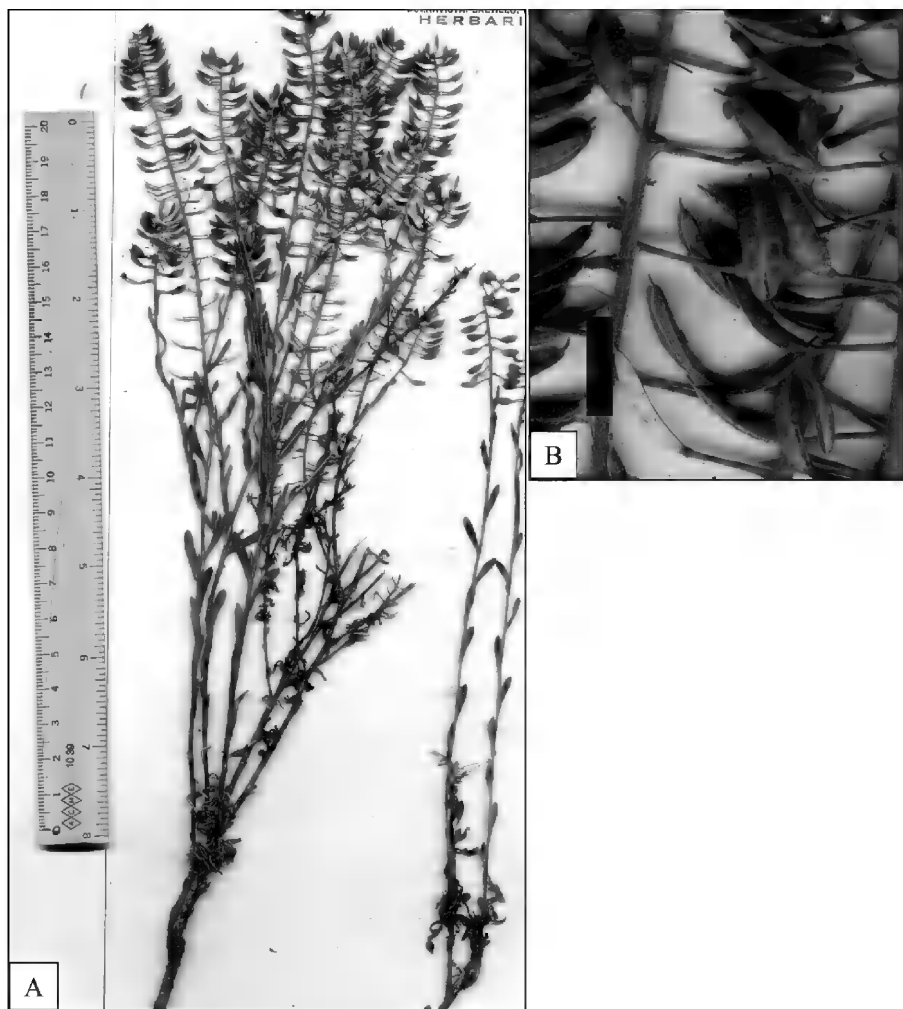
Figure 6. *Sphaerocardamum compressum* (*Villarreal & Carranza 3773* [ANSM]). A) General habit. B) Close-up of fruit and infructescence (scale = 5 mm).
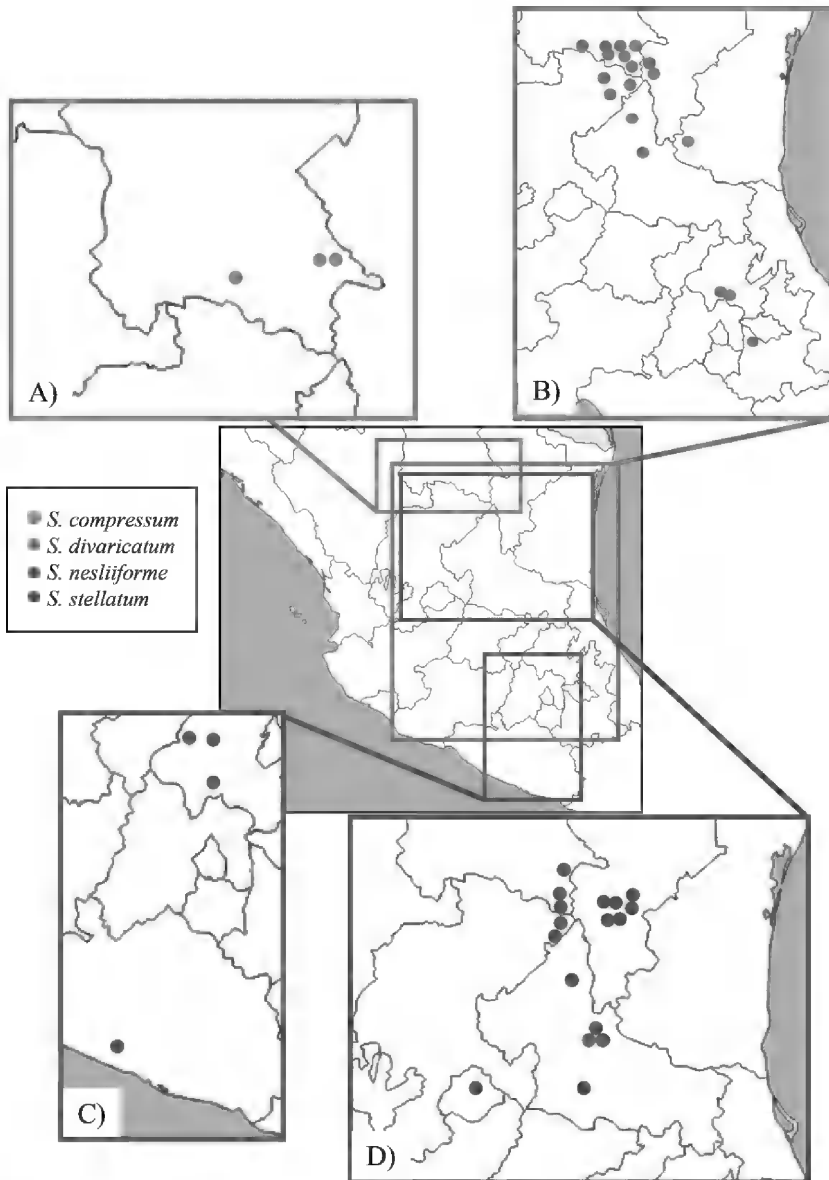
Figure 7. Distribution Maps. A) *S. compressum* (blue inset). B) *S. divaricatum* (red inset). C) *S. nesliiforme* (green inset). D) *S. stellatum* (purple inset). All base maps from http://d-maps.com/m/america/mexico/mexique/mexique15.gif

        Additional collections examined. MEXICO. Coahuila. Las Vigas, Cañon de la Carbonera, Sierra de Arteaga 25º 20' N, 100º 39' W, 2100-2600 m, no date, *Villarreal & Carranza 3773* (ANSM); along the road that parallels the railroad tracks from Parras to Saltillo, 49 km E of Parras, 14 km W of the deviation to El Cinco (on some maps "Cinco de Mayo"), uphill side of the road (S), 2085 m, 30 Aug 1997, *Bailey & Ochoterena 97* (MEXU); Mpio. Arteaga, Sierra de Arteaga, Cañon de Jamé, 8 km past (E) of Jamé turn left on a small road to the residence Las Vigas, 2 km up the road, 25º 21' 312'' N 100º 33' 741'' W, 2850 m, 2 Sept 1997, *Bailey & Ochoterena 104* (BH, MEXU); Mpio. Arteaga, Sierra de Arteaga, small stone road leading from El Tunal to Arteaga, N25° 26' 599'' 100° 37' 593'' W, 2380 m, 2 Sep 1997, *Bailey & Ochoterena 115* (BH, MEXU).

2. SPHAEROCARDAMUM **DIVARICATUM** (Rollins) Rollins, Contrib. Gray Herb. 213: 16. 1984.
        Cibotarium divaricatum Rollins, Contrib. Dudley Herb. 3: 189-190, 1941. **TYPE: MEXICO**.
        Coahuila. Sierra de Parras, *Purpus 1027* (holotype: GH!; isotype NY! UC!). Figs. 7 & 8.

        Sphaerocardamum macropetalum (Rollins) Rollins, Contrib. Gray Herb. 213: 16. 1984.
        Cibotarium macropetalum Rollins, Contrib. Dudley Herb. 3: 190-191. 1941. **TYPE:**
        MEXICO. **Zacatecas**. Near Concepción del Oro, 11-14 Aug 1904, *Palmer 297* (holotype:
        GH!; isotypes: MO!, NY!, UC!, US!).

        Biennial or perennial, 3-45 cm tall. **Stems** erect, branched below and within the inflorescence, moderately to densely pubescent. **Leaf** margins entire to denticulate, trichomes with 4-11 ramifications. **Inflorescence** compound. **Pedicels** divaricately ascending, 2.0-10 mm long. **Perianth** widely spreading. **Sepals** 1.0-1.8 mm long and 0.45-1.0 mm wide. **Petals** spatulate with distinct claw and blade, 1.2-2.9 mm long and ca. 0.6-1.6 mm wide at the distal end. **Filaments** 1.0-2.8 mm long; **anthers** pale to purple. **Gynoecium** oblong, often protogynous with styles protruding beyond the apex of the closed buds; **ovules** 4 (rarely 3)-8 (rarely as many as 11) per locule. **Fruit** oblong, weakly angustiseptate, 2.5-6.1 mm long, 1.0-2.5 mm wide, 0.8-2 mm deep; minute apical notch absent; **styles** 0.5-2.0 mm long; **stigmas** obscurely bilobed; **valves** unkeeled to slightly keeled, densely pubescent on the exterior, moderately to densely pubescent on the interior. **Seeds** biseriately arranged, 4 (rarely 3)-8 (rarely as many as 11) per locule, 0.85-1.4 mm long and 0.5-0.8 mm wide. *n* = 8.

        Phenology. Flowering March to November.

        Sphaerocardamum divaricatum is distinguished from the other *Sphaerocardamum* by its oblong largely unkeeled fruits, large petals with expanded blades, internally pubescent fruit valves, and fruits lacking an apical notch below the style. The morphological distinctions between Rollins's (1984) *S. divaricatum* and *S. macropetalum* were not supported when considering information from newer collections.

        Sphaerocardamum divaricatum is a widespread taxon, with populations in Coahuila, Nuevo León, Puebla, San Luis Potosí, Tamaulipas, and Zacatecas (Fig. 7) at elevations ranging from 1800-2900 m. This distribution overlaps slightly with *S. compressum* and *S. nesliiforme* and more extensively with *S. stellatum*. Populations of *S. divaricatum* have been noted growing on limestone soils with *Acacia, Agave, Dasylirion, Larrea, Pinus cembroides, Opuntia*, and *Salvia*.

        Additional collections examined. MEXICO. Coahuila. Limestone ledges on Carneros Pass, 9 Sep 1889, *Pringle 2848* (GH); Municipio de Saltillo, Estacion Carneros Camino, torre de
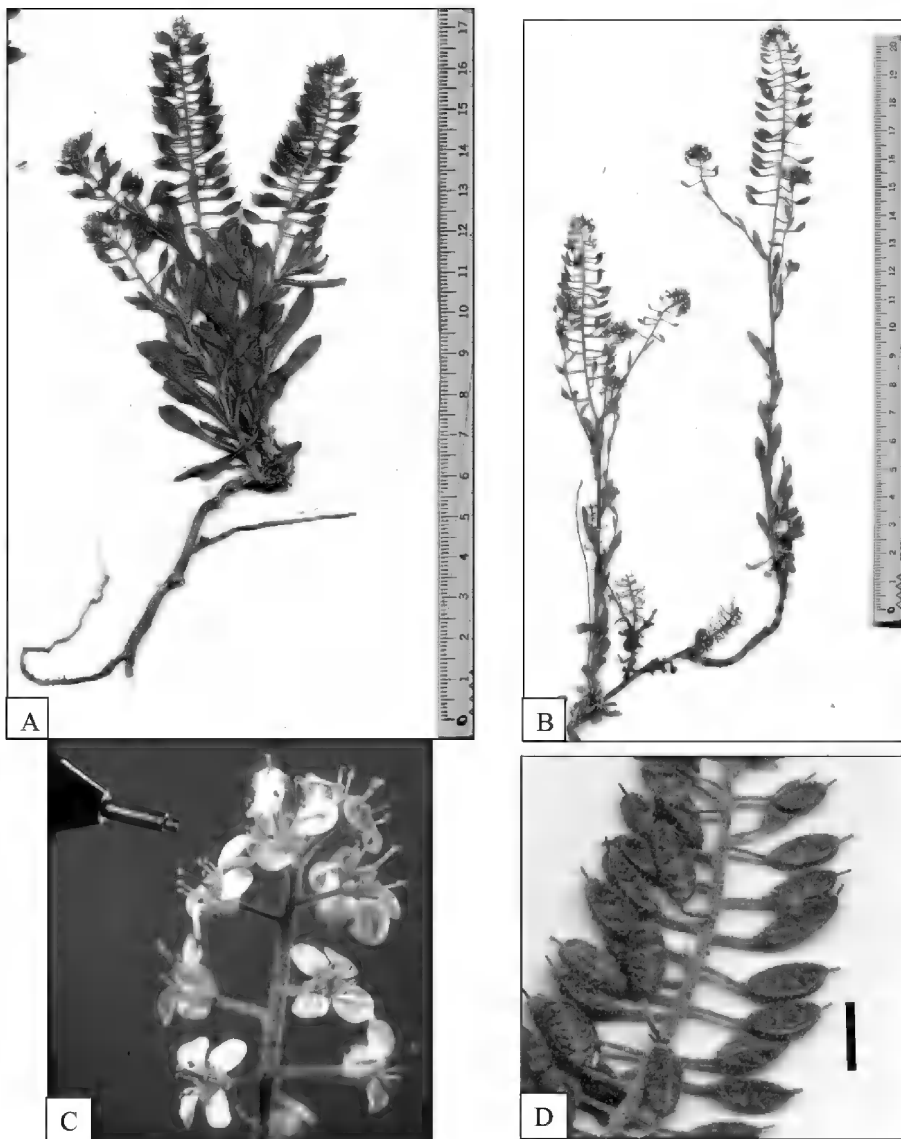
Figure 8. *Sphaerocardamum divaricatum.* A) Habit (*Rollins & Ruby 74137* [GH]). B) Habit (*Hinton 21852* [TEX]). C) Inflorescence (*Bailey & Ochoterena 99* [BH & MEXU]). D) Infructescence (*Rollins & Ruby 74137* [GH]) – scale = 5 mm.

microndas, 3 km al Poniente de la Estacion, 30 km Al Sur de Saltillo, 25° 07' 30" N 101° 07' W, 2100 m, 24 May 1982, *Villarreal s.n.* (ANSM); ca. 2 km N of Estación Carneros, E flank of Sierra El Chorreadero, 2150 m, 29 Mar 1973, *Johnston, Wendt, & Chiang 10497A* (TEX); Carneros Pass, 26 mi S of Saltillo, 7200 ft, 18 Nov 1958, *Rollins & Tryon 58134* (GH, MO NY, TEX, UC, US); belt in a mountain valley, about 4 mi E of Carneros Pass, on road to Hedionda Grande, 2 May 1959, *Correll & Johnston 21325* (GH, NY, TEX); rock crevices on steep hillside, first pass S of Carneros Pass, 29 mi S of Saltillo near Mex. Hwy. 54, 29 Sep 1974, *Rollins & Roby 7489* (ENCB, GH, MO, NY, US); Carneros Pass, limestone ledges, 12 Aug 1890, *Pringle 3195* (BM, GH, KEW, NY, TEX, UC, US); Sierra de Parras en el Capulín, 2050 m, 9 Jun 1981, *Rodríguez & Carranza 861* (ANSM); Saltillo and vicinity, Jun & Sep 1898, *Palmer 347* (BM, GH, MO, NY, UC, US); Fraile, 59 km S of Saltillo, in playa valleys with some considerable drainage from surrounding hills, 1967 m, 10 Jul 1941, *Stanford, Retherford, & Northcraft 290* (GH, MO); ca. 2-3 km up the road to the radio tower from Estación Carneros (Carneros Pass), 2200 m, 6 Sep 1997, *Bailey & Ochoterena 133* (BH, MEXU); 16 mi S of Arteaga, 18 Aug 1948, *Kenoyer & Crum 2807* (GH); Mpio. G. Cepeta, 63 km E of Parras, take the deviation south toward El Cinco (on some maps "Cinco de Mayo") 18 km (as you pass through El Tejocote keep to the left, plants in canyon "Boca de Domingo"), 2050 m, 30 Aug 1997, *Bailey & Ochoterena 102* (MEXU); Mpio. G. Cepeta, 63 km E of Parras take the deviation S toward El Cinco (on some maps "Cinco de Mayo") 14 km (as you pass through El Tejocote keep to the left, plants in canyon "Boca de Domingo, 2000 m, 30 Aug 1997, *Bailey & Ochoterena 99* (BH, MEXU); along the road that parallels the railroad tracks from Parras to Saltillo, 49 km E of Parras, 14 km W of the deviation to El Cinco (on some maps "Cinco de Mayo"), 2085 m, 30 Aug 1997, *Bailey & Ochoterena 93* (BH, MEXU); Carneros Pass, 26 mi S of Saltillo, 1885 m, *Bailey 45* (MEXU); valley 15 km W of Concepción del Oro just within Coahuila border, 2300 m, 19 Jul 1941, *Stanford, Retherford, & Northcraft 484* (GH, MEXU, MO, NY, UC); Coahuila/Zacatecas boarder, 9 km S of Parras on Sierras Negras, 3 Jul 1941, *Stanford, Retherford, & Northcraft s.n.* (NY). **Hidalgo**. El Capulin, near km 134 on highway between Actopan and Ixmiquilpan, 1800 m, 4 Aug 1948, *Moore & Wood 4253a* (GH); just S of Patria Nueva, 16 km N of Actopan near Mex. Hwy 85, 17 Oct 1983, *R. & K. Rollins with Sousa-Pena 83347* (ENCB, GH). **Nuevo León**. San Urbert, 1900 m, 20 Mar 1992, *Hinton 21852* (TEX); S.J. Las Joyas, 2420 m, 29 Jun 1983, *Hinton 18499* (TEX); low hill near Hwy. 57, 34 mi S of Saltillo, 5 Sep 1976, *Rollins & Roby 76065* (GH); 4 mi S of the turn-off to Hacienda de San Jose Raices, between Saltillo and Matehuala, 20 Nov 1958, *Rollins & Tryon 58181* (GH); 1.5 km E of El Barrosito, 1.5 km W of Puero Prieta in southern part of Sierra la Tomita, 2100 m, 19 Jun 1972, *Wendt, Chiang, & Johnston 8008* (GH). **Puebla**. Traveling from Puebla to Tehuacan turn off main Hwy 150 to Hwy 150 for Orizaba, plants found on N-facing slope ca. 200 m down the road from the interchange, 2120 m, 13 Jul 1996, *Bailey 15* (BH, MEXU). **San Luis Potosí**. Ca. 6 km al E de laguna seca Mpio. de Charcas, 2150 m, 10 Sept 1955, *Rzedowski 6551=628* (ENCB, MO, TEX); 2 km S on the road to Real de Catorce from the road between Matehuala and San Francisco de los Quijano, 2280 m, 8 Sep 1997, *Bailey & Ochoterena 138* (MEXU). **Tamaulipas**. 6 km al S de Bustamante, 1950 m, 15 Aug 1972, *Lopez y Dirzo 4651* (MEXU); Patria Nueva, 1 km S of town along interstate 85, N of Pachuca, 1980 m, 12 Sep 1997, *Bailey & Ochoterena 158* (BH, MEXU). **Zacatecas**. Sierra del Astillero (approached from the SE, from Tanque El Alto), 2500-3195m, 2 Jul 1973, *Johnston, Wendt, & Chiang 11551C* (TEX); 5.5 km by road E of Salaverna toward Concepción del Oro, 3 km W of Aranzazu, N side of pass in mountains, 2900 m, 29 Mar 1973, *Johnston, Wendt, & Chiang 10475A* (TEX); 4 km E of Salaverna, S side of a mountain pass, 2900 m, 29 Mar 1973, *Johnston, Wendt, & Chiang 10473A* (GH, TEX); hillside, 9.6 mi W of Concepción del Oro, 8 Oct 1974, *Rollins & Roby 74137* (ENCB, GH, MO, NY, US); Concepción del Oro, Sierra Madre Oriental, 2300-2700 m, 18-19 Jul 1934, *Pennell 17399* (GH, NY, US); ca. 16 air mi E of Concepción del Oro, 3 mi NE of Guadalupe Garceron in small igneous canyon of main canyon of Sierra del Astillero, 6350 ft, 22 Sep 1973, *Henrickson 13289* (GH); Sierra del Astillero (approached from SE, from Tanque El Alto), 2100-3195 m, 2 Jul 1973, *Johnston, Wendt & Chiang 11564* (GH, MEXU, TEX); Puerto de Rocamontes at the Zacatecas-Coahuila state line, 1990 m, 29 Mar 1973, *Johnston, Wendt, & Chiang*

10487 (GH, TEX); 1.5 km ESE of Salaverna, on road to Concepción del Oro, 2800 m, 17 Jun 1972, *Chiang, Wendt & Johnston 7936* (GH, TEX); ca. 2 km E of Salaverna, 14 km W of Concepción del Oro, 2600 m, 7 Sep 1997, *Bailey & Ochoterena 137* (BH, MEXU); K884-S of Saltillo, 29 July 1929, *Runyon 1333* (TEX, US).

3. **S**PHAEROCARDAMUM **NESLIIFORME** S. Schauer, Linnaea 20: 720 1847. **TYPE: MEXICO.** Locality unknown, *Aschenborn 209* (holotype: B!). Figs. 7 & 9.

Cibotarium microcarpum Rollins, Rhodora 59: 70. 1957. **TYPE: MEXICO.** District of Zimapán, dry rocky slopes of Barranca de Tolimán somewhat above the mines, 7.6 mi from Zimapán on road to Mina Loma del Toro and Balcones, 5000 ft, 30 Oct 1949, *H.E. Moore Jr. 5443* (holotype GH!; isotype BH!).

Biennial, 8-35 cm tall. **Stems** erect, mostly distally branched. **Leaf** margins denticulate to dentate, trichomes with 2-6 ramifications. **Inflorescence** compound. **Pedicels** divaricately ascending, 2-6 mm long. **Perianth** spreading. **Sepals** 0.5-1 mm long and 0.3-0.6 mm wide. **Petals** narrowly oblanceolate, little distinction between claw, blade 0.6-1.1 mm long and 0.125 -0.25 mm wide. **Filaments** 0.65-1.4 mm long; **anthers** purple or pale. **Gynoecium** spherical; often protogynous with styles protruding beyond the apex of the closed buds; **ovules** 2 (rarely 3) per locule, one attached on each side of the replum near the apex. **Fruit** spherical, uncompressed 0.9-1.9 mm in diameter; minute apical notch absent; **styles** 0.5-0.9 mm long; stigmas obscurely bilobed; **valves** rounded on the back, densely pubescent on the exterior, sparsely to moderately pubescent on the interior. **Seeds** 2 (rarely 3) per locule, 0.6-0.8 mm long and 0.4-0.5 mm wide. $n = 8$.

Phenology: Flowering in October (based on limited information).

Sphaerocardamum nesliiforme is easily distinguished by the 2 (rarely 3) seeds per locule and spherical fruits. The current study supports Rollins's (1984) decision to synonymize *Cibotarium microcarpum* and *S. nesliiforme*. Geographically *S. nesliiforme* is restricted (Fig. 7) to the southernmost range for *Sphaerocardamum,* with collections only known from limestone soils in mountainous areas of Hidalgo and a single disjunct locality in Guerrero. The distribution for *Sphaerocardamum nesliiforme* only overlaps slightly with that for *S. divaricatum,* and these two have only been collected growing sympatrically from a single locality. Populations grow at elevations from 1100-2000 m in association with *Acacia, Croton, Juniperus, Karwinskia, Pinus,* and *Yucca.*

Additional collections examined. **MEXICO. Guerrero.** Mpio. Atoyac de Alvarez, El Ranchito, 1100 m, 19 Aug 1985, *Soto Nunez & Roman 10087* (MEXU). **Hidalgo**. Mpio. Zimapán, along a little used mining road, steep SE slope of Barranca de Toliman, 7.6 mi N of Zimapán, 18 Oct 1983, *Rollins & Sousa-Pena 83349* (ENCB, GH); road from Ixmiquilpan to Tolontongo above the first 180° corner as you decend into Barranca de Tolantongo, 22 km NE of Ixmiquilpan, 12 km NE of Cardonal, 6 km NE of San Cristobal, 1850 m, 10 Sep 1997, *Bailey &Ochoterena 152* (BH, MEXU); from Zimapán follow the mining road toward the mines in Barranca de Tolimán, ca. 8 km N of Zimapán turn right onto a (currently) less well used road, 2 km up this road you cross over a small pass and immediately after turn left down an abandon road ca. 1 km on uphill side of the road, 1760 m, 11 Sep 1997, *Bailey & Ochoterena 156* (BH, MEXU); Patria Nueva, 1 km S of town along Interstate 85, N of Pachuca, 1980 m, 12 Sep 1997, *Bailey & Ochoterena 157* (BH, MEXU)**.**
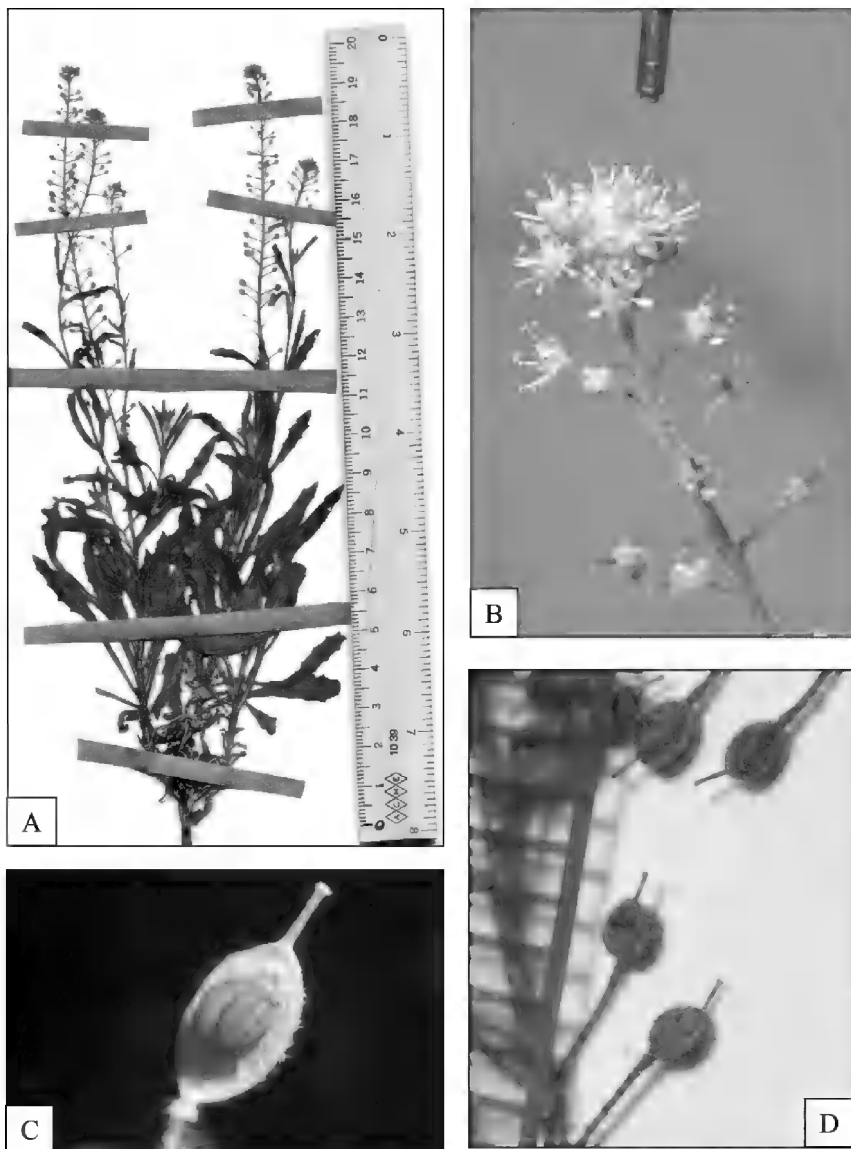
Figure 9. *Sphaerocardamum nesliiforme*. A) Habit (*Rollins 83349* [GH]). B) Inflorescence (*Bailey & Ochoterena 157* [BH & MEXU]). C) Open fruit with intact seeds (*Bailey & Ochoterena 157* [BH & MEXU]). D) Infructescence (*Rollins 83349* [ENCB]).

4. SPHAEROCARDAMUM STELLATUM (S. Wats.) Rollins, Contrib. Gray Herb. 213: 14. 1984. *Cibotarium stellatum* (S. Wats.) O.E. Schulz, Engl. Jahrb. 66: 91. 1933. *Capsella stellatum* S. Wats., Proc. Amer. Acad. 25: 142. 1890. **TYPE: MEXICO. Coahuila**. Limestone ledges on Carneros Pass, 9 Sep 1889, *Pringle 2844* (holotype: GH!). Figures. 7 & 10.

Sphaerocardamum fruticulosum (Rollins) Rollins, Contrib. Gray Herb. 213: 14-15. 1984. *Cibotarium fruticulosum* Rollins, Contrib. Dudley Herb. 3: 187. 1941. **TYPE: MEXICO. San Luis Potosí**. Minas de San Rafael, Jun 1911, *Purpus 5374* (holotype: GH!; isotype NY!, US!).

Sphaerocardamum macrum (Standl.) Rollins, Contrib. Gray Herb. 213: 15. 1984. *Cibotarium macrum* Rollins, Contrib. Dudley Herb. 3: 189. 1941. *Lepidium macrum* Standl., Publ. Field Mus. Nat. Hist., Chicago, Bot. Ser. 17: 248. **TYPE: MEXICO. Nuevo León.** Muncipio de Derrumbadero, Cañon de los Capulines, above San Enrique, Hacienda San Jose de Raices, 6 Aug 1935, *Mueller 2411* (holotype: F; isotypes GH!, MO!).

Sphaerocardamum ramosum Rollins, Contrib. Gray Herb. 213: 15. 1984. **TYPE: MEXICO. Nuevo León**. Cerro Potosí, E slope, dry rocky open places between corn fields, 6050 ft, 9 Jul 1963, *MacGregor, Harms, Robinson, Rosaria & Segal 413* (holotype: GH!).

Biennial or perennial, 4-40 cm tall. **Stems** erect, branched below and within the inflorescence. **Leaf** margins entire to dentate; trichomes with 1-7 ramifications. **Inflorescence** compound. **Pedicels** divaricately ascending to slightly descending, 1-7 mm long. **Perianth** widely spreading to somewhat closed. **Sepals** 0.6-1.4 mm long and 0.3-0.9 mm wide. **Petals** strap shaped to spatulate (limited distinction between claw and blade), 0.4-1.6 mm long and ca. 0.1-0.65 mm wide at the distal end. **Filaments** 0.4-1.8 mm long; **anthers** pale to purple. **Gynoecium** obovate, sometimes protogynous; **ovules** 4 (rarely 3) -8 per locule. **Fruit** obovate, strongly angustiseptate, 1.8-4.6 mm long, 1.0-2.9 mm wide, 0.6-2.2 mm deep; minute apical notch often present; **styles** 0.2-1.1 mm long; stigmas capitate to obscurely bilobed; **valves** keeled, densely pubescent on the exterior, pubescent on the interior (sometimes individual fruits with glabrous valves); septum complete or slightly perforate. **Seeds** biseriately (occasionally nearly uniseriately) arranged, 3-8 per locule, 0.4-1 mm long and 0.3-0.75 mm wide. $n = 8$.

Phenology. Flowering March to November.

Sphaerocardamum stellatum is recognized by its obovate keeled fruits, short styles and petals. Populations are known from Aguascalientes, Coahuila, Nuevo León, San Luis Potosí, and Zacatecas (Fig. 7), making it another widespread species. Its range only overlaps with *S. divaricatum*, but it has been collected growing sympatrically with this species at three different localities. Habitats for *S. stellatum* typically include limestone soils from 1555-2470 m in association with *Acacia, Agave, Dasylirion, Larrea, Pinus cembroides, Opuntia*, and *Toxicodendron*.

Additional collections examined. MEXICO. Aguascalientes. Ladera S del Cerro Palmira, 4 km al W de Asientos, 2300 m, 1 Nov 1967, *Rzedowski 25059* (ENCB). **Coahuila**. MEX 57 ca. 9 km SE of the deviation to Huachichil and 2 km NW of the border with Nuevo León, NW-facing slope on W side of road, 2080 m, 3 Sep 1997, *Bailey & Ochoterena 120* (BH, MEXU); Saltillo and vicinity, June 1898, *Palmer 347* (BM, US); Saltillo and vicinity, 1898, *Palmer 347.5* (UC); Saltillo, 10 Aug 1905, *Palmer 752* (GH, NY); limestone ledges on Carneros Pass, 9 Sep 1889, *Pringle 2844* (GH); limestone ledges, Carneros Pass, 12 Aug 1890, *Pringle 3195* (K); rock crevices first pass S of Carneros Pass, 29 mi S of Saltillo near Mex. Hwy 54, 29 Sep 1974, *Rollins & Roby 7490* (GH, NY); ravine, Carneros Pass, 26 mi S of Saltillo, 7200 ft, 18 Nov 1958, *Rollins & Tryon 58133* (MO, NY, TEX, UC, US); ca. 2 km N of Estacion Carneros, E flank of Sierra El Chorreadero, 2150m, 29 Mar
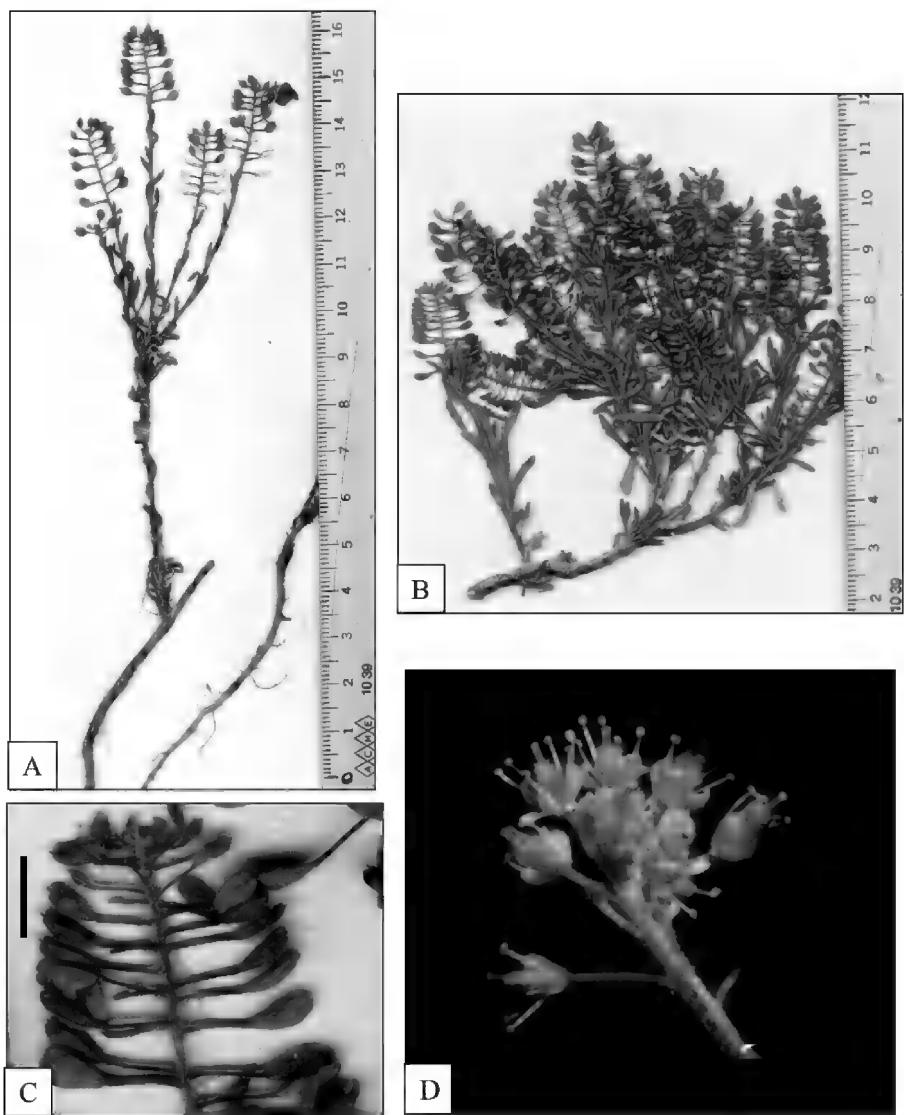
Figure 10. *Sphaerocardamum stellatum*. A) Habit (*Wells & Nesom 99* [LL]). B & C) Habit and infructescence (*Chiang et al. 8143* [LL]), scale = 5 mm. D) Inflorescence.

1973, *Johnston, Wendt, & Chiang 10497A* (GH, TEX); Cuesta de Palmas Altas, 2250 m, 21 Aug 1975, *Robert & Passini s.n.* (ANSM); Rancho Demonstrative "Los Angeles" 34 km al S de Saltillo, Aug 1972, *collector unknown s.n.* (ANSM); 16 mi S of Arteaga, 18 Aug 1948, *Kenoyer & Crum 2807* (GH). **Nuevo León**. Dirt road ca. 2 km WSW of San Pablo, 16 km E of San Rafael on the road between San Pablo and San Rafael, 2400 m, 3 Sep 1997, *Bailey & Ochoterena 122* (BH, MEXU); Hwy 58 between San Roberto and Linares, km marker 54, 10 km W of Iturbide, 1 km E of the deviation to Las Delicias, 1780 m, 5 Sept 1997, *Bailey & Ochoterena 131* (MEXU); Cerro Potosí, 19 km NE of Galeana, 3 km up the road to radio tower on the mountain, gradual E-facing slope, 2130 m, 4 Sep 1997, *Bailey & Ochoterena 125* (BH, MEXU); 20 km NW of Galeana, 4 km NW of Marzo on the road from Marzo to La Lagunita, above the very steep roadcut, 2170 m, 4 Sep 1997, *Bailey & Ochoterena 126* (BH, MEXU); 37 km NW of Galeana, 3 km NE of the deviation to San Jose de la Joya on the road between Galeana and Los Mimbres (km marker 13.5), 2470 m, 4 Sep 1997, *Bailey & Ochoterena 128* (BH, MEXU); 7 km E of Cienaga del Toro on the road to Santa Rosa and Rayones, 1980 m, 4 Sep 1997, *Bailey & Ochoterena 130* (BH, MEXU); 3 km SE of Santa Clara de Gonzáles on a dirt road to San José de Raices, S.C. de Gonzáles is ca. 20 km S of Galeana, 2130 m, 5 Sep 1997, *Bailey & Ochoterena 132* (BH, MEXU); Iturbide to Camarones, 1570 m, 13 Sep 1991, *Hinton 21455* (TEX); low hills E of Hwy 57, turn-off to La Boca, 177 km N of Matahuala, 5 Sep 1976, *Rollins & Roby 76067* (ENCB, GH2, US); 8 km S of Galeana at fork in the road to Dr. Arroyo and San Roberto, small limestone hill 300 m W of junction, 1630 m, 29 Jul 1996, *Bailey 57* (BH, MEXU); 15 mi E of San Rafael off Hwy 57, 100° 26' W 25° 03' N, ca. 1 mi WSW of San Pablo in narrow valley, 8000 ft, 22-23 July 1977, *Wells & Nesom 99* (GH, LL); Sierra Madre Oriental, San Francisco Canyon, about 15 SW of Pueblo Galeana, 7500-8000 ft, 12 May 1934, *C.H. & M.T. Mueller 317* (AA); on Route 60 at the village of Iturbide, 8 Oct 1962, *Turner & Powell 1070* (TEX); 1-2 mi SW of Pablillo, 21 Jul 1958, *Correll & Johnston 1929* (TEX); arid calcareous-gypseous hillside in thin pine-pinyon woodland, 9 mi W of Galeana, 13 Nov 1964, *Ripley & Barneby 13800* (NY); Galeana to Rayones + 19 km, Rayones, 1560 m, 20 Oct 1990, *Hinton et al. 20831* (GH, TEX). **San Luis Potosí**. Hwy 57, 1 km N of Charco Blanco, then 200 m up the small road to the statue of Benito Juárez, plants on the steep N-facing slope adjacent to the parking lot, 1650 m, 8 Sep 1997, *Bailey & Ochoterena 141* (BH, MEXU); road between Moctezuma and San Lorenzo, 2 km W of Salitrillos (21 km E of Arista), S side of the road at the base of a hill, 8 Sep 1997, *Bailey & Ochoterena 140* (MEXU); Hwy 57, 1 km N of Charco Blanco, then take the road going E toward Guadalcázar for 2 km, 1645 m, 8 Sep 1997, *Bailey & Ochoterena 142* (BH, MEXU); 9 km N of San Jose and ca. 10 km S of Armadillo (Armadillo de los Enfantes), 2045 m, 9 Sep 1997, *Bailey & Ochoterena 144* **(**BH, MEXU**)**; Minas de San Rafael, Jun 1911, *Purpus 5235* (BM, UC); Minas de San Rafael, Jul 1911, *Purpus 5235'* (UC); ca. 12 km al SE de Armadillo, ca. 2000 m, 10 Aug 1956, *Rzedowski 7964* (ENCB); steep hillside, 50 mi NE of San Luis Potosí on the road to Matehuala, 5100 ft, 21 Nov 1958, *Rollins & Tryon 58191* (GH, MO, NY, TEX, UC, US); 6 km E of Estación Catorce on the winding road to Real de Catorce, NW portion of the Sierra de Catorce, 2160 m, 17 May 1973, *Johnston, Wendt, & Chiang 11078D* (TEX); 7.4 km E of the San Luis Potosí-Matehuala highway on the road to Cerritos, 1800 m, 29 Jun 1972, *Chiang, Wendt & Johnston 8143* (TEX). **Zacatecas**. Ca 15 (air) mi E of Concepción del Oro, 2.5 mi NE of Guadalupe Garceron in small ravine NW of summit of igneous Sierra del Astillo, 6500 ft., 22 Sep 1973, *Henrickson 13302 B* (GH); Municipio de Saltillo a 60 km, carretera a Concepción del Oro, Rancho "Dos Arbolitos," 15 Aug 1981, *Vásquez, Tersa, & de León s.n.* (ANSM).

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HANDROANTHUS ×LEWISII (BIGNONIACEAE), A NEW HYBRID FROM CULTIVATION

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ABSTRACT

Handroanthus ×lewisii, an unusually handsome hybrid of *Handroanthus heptaphyllus* and *H. umbellatus* (trumpet trees, Bignoniaceae), is now well established at the Los Angeles County Arboretum and Botanic Garden in Arcadia, California, near Los Angeles, where it was first developed, and at several other locations in Southern California. Because it is gaining in popularity and might soon be marketed to retail nurseries, we provide formal botanical and common names for this hybrid.

Handroanthus Mattos comprises arguably the showiest winter- and spring-flowering trees in Southern California. Established in 1970 (Mattos 1970), the genus includes about 30 species of trees from Mexico to Argentina (Grose & Olmstead 2007) that most authors (e.g., Gentry 1992) previously included in *Tabebuia* Gomes ex. DC. Indeed, *Handroanthus* was largely unaccepted until the publication of Grose and Olmstead in 2007. When Mattos (1970) segregated out *Handroanthus*, he noted that it differed from *Tabebuia* in its palmately compound leaves and eight to nine ovules/locules per ovary (vs. simple leaves and three to four ovules/locules per ovary in *Tabebuia*). However, Gentry (1972, 1992) insisted that *Tabebuia* was a natural lineage and should not be divided, and he was loathe to accept *Handroanthus*, which he never did. Based on more recent molecular studies, Grose and Olmstead (2007) divided *Tabebuia* into three genera: (1) *Handroanthus*, comprising mostly yellow-flowered species with various degrees of hairs covering the leaves and calyx and extremely dense wood containing large quantities of lapachol; (2) *Roseodendron* Miranda, including just two species having spathaceous calyxes with a texture similar to that of the corolla; and (3) *Tabebuia*, restricted to species having white to red or rarely yellow flowers with stalked or sessile lepidote scales.

Figure 1. *Handroanthus* includes the most spectacular winter- and spring-flowering trees in southern California, as here with *H. heptaphyllus*, the pistillate parent of *H. ×lewisii* (Whittier, California) (© D.R. Hodel).

The two most common species in Southern California are (1) the pink-flowered *Handroanthus heptaphyllus* (Vell.) Mattos [*Tabebuia heptaphylla* (Vell.) Toledo], heretofore known as *H. impetiginosus* (Mart. ex DC.) Mattos [*T. impetiginosa* (Mart. ex DC.) Standl.], a name misapplied to material in Southern California and perhaps elsewhere (Hodel et al. 2015) (Fig. 1) and (2) the yellow-flowered *H. chrysotrichus* (Mart. ex DC.) Mattos [*T. chrysotricha* (Mart. ex DC.) Standl.]. The Los Angeles County Arboretum and Botanic Garden in Arcadia is primarily responsible for introducing these two species to the southern California nursery trade and landscape, where they are popularly known as pink or yellow trumpet trees (respectively) or pink or yellow tabs, the latter word being an abbreviated derivation of their former genus name. Other species sometimes encountered and mostly confined to botanical gardens and arboreta include the yellow-flowered *H. ochraceus* (Cham.) Mattos [*T. ochracea* (Cham.) Standl.] and *H. umbellatus* (Sond.) Mattos [*T. umbellata* (Sond.) Sandwith] (Fig. 2). *Tabebuia* still exists, though, and includes 67 species, one of which, the pink flowered *T. heterophylla* (DC.) Britton, is in the desert plant collection in Balboa Park in San Diego.

The extremely variable but typically larger *Handroanthus heptaphyllus* can flower from November through April with a peak in February and March while the other species, mostly yellow-flowered and generally of smaller habit flower mostly in February and March. Because they bloom in dense, large, many-flowered clusters at the ends of bare branches when most or all of the leaves have dropped, they are nothing short of spectacular and garner much well deserved attention when in full flower.

Figure 2. *Handroanthus umbellatus,* the staminate parent of *H. ×lewisii,* is one of the yellow-flowered species in the genus (Los Angeles County Arboretum and Botanic Garden, *1967-1455-P*3*) (© D.R. Hodel).

In 1970, the late George Lewis, a senior gardener at the Los Angeles County Arboretum and Botanic Gardens, first made the hybrid (now popularly known as the apricot tab) between *Handroanthus heptaphyllus* (he referred to it as *Tabebuia   impetiginosa*) and, as it turns out, *H. umbellatus*. However, the identity of one of the latter parent was not specified and has only recently been resolved. Lewis's records clearly show that *H. impetiginosus* (*1955-2559-S*, ex Porto Allegre, Brazil) was the pistillate (seed) parent. Unfortunately, he did not specify the staminate (pollen) parent; however, because *H. chrysotrichus* was by far the most common yellow-flowered taxon in the Arboretum at the time, we initially assumed it was the staminate parent. At least four accessions from 1953 to 1966 totaling 24 plants of *H. chrysotrichus*, which possibly would have been sufficiently mature to flower by 1970, were extant in the Arboretum as late as 2007. In contrast, one accession from 1953, totaling two plants of *H. ochraceu*s and three accessions from 1966 to 1968, totaling five plants of *H. umbellatus*, which possibly would have been sufficiently mature to flower by 1970, were extant in the Arboretum as late as 2007. The Arboretum featured and promoted *H. chrysotrichus* in particular, formally introducing it to the nursery trade in April 1964. Another possibility is that the staminate parent was not even at the Arboretum and Lewis had pollen sent to him from elsewhere.

Nonetheless, and despite this seemingly overwhelming evidence favoring *Handroanthus chrysotrichus* as the staminate parent, we became suspicious of this parentage when comparing the habit and leaf indumentum of the hybrid with its putative staminate parent. Coauthor Greby first noted that the branching structure of the hybrid was much more similar to that of *H. umbellatus* than that of *H. chrysotrichus*. The hybrid and *H. umbellatus* tend to have two to three strongly co-dominant leaders while *H. chrysotrichus* has a more central leader. Also, the smaller, much less hairy leaflets of the hybrid are more similar to those of *H. umbellatus*. These suspicions prompted us to look for a more definitive resolution of the staminate parent. We determined the staminate and confirmed the pistillate parents of the hybrid by comparing DNA sequences (ITS2) of four candidate parents with that of samples from two hybrid trees, one from the Arboretum's original cross and one from a landscape street tree of unknown origin in Whittier, California, about 40 km distant. At three positions where the candidate parents differ from each other, the hybrids display a sequence trace resulting from the combination of the two parents (*H. heptaphyllus* and *H. umbellatus*) (Figs. 3A and B, 4A and B).

Figure 3. A comparison of DNA sequences (5.8S-ITS2) from four parental candidates to that of the hybrid *Handroanthus x lewisii* (Hxl-1) at the Los Angeles County Arboretum and Botanical Garden, Arcadia, California. *Handroanthus hepataphyllus* was known to be one of the parents.
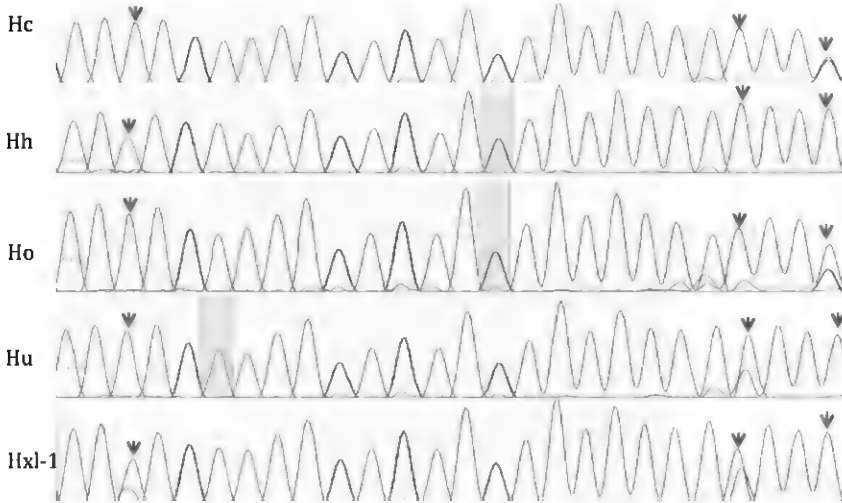
A. Sequence traces of four parental candidates and the hybrid. Arrows point to three positions, which show variations among the potential candidates. The hybrid Hxl-1 shows a combined trace for *H. heptaphyllus* and *H. umbellatus.* Hc, *H. chrysotrichus;* Hh, *H. heptaphyllus;* Ho, *H. ochraceus;* Hu, *H. umbellatus.*
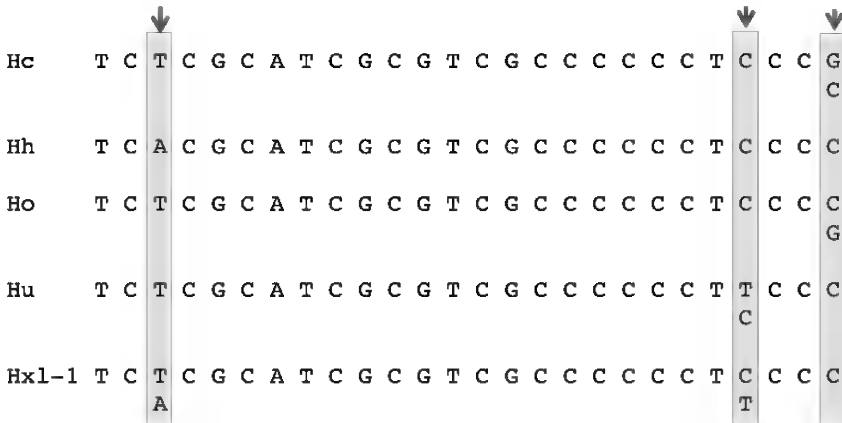
B. Translation of the traces to nucleotide sequences. Arrows point to the three positions identified in part A. The hybrid Hxl-1 shows a combined sequence for *H. heptaphyllus* and *H. umbellatus.* Hc, *H. chrysotrichus;* Hh, *H. heptaphyllus;* Ho. *H. ochraceus;* Hu, *H. umbellatus.*

Figure 4. A comparison of DNA sequences (5.8S-ITS2) from four parental candidates to that of the hybrid *Handroanthus x lewisii* (Hxl-2) at Whittier, California. *Handroanthus hepataphyllus* was known to be one of the parents.
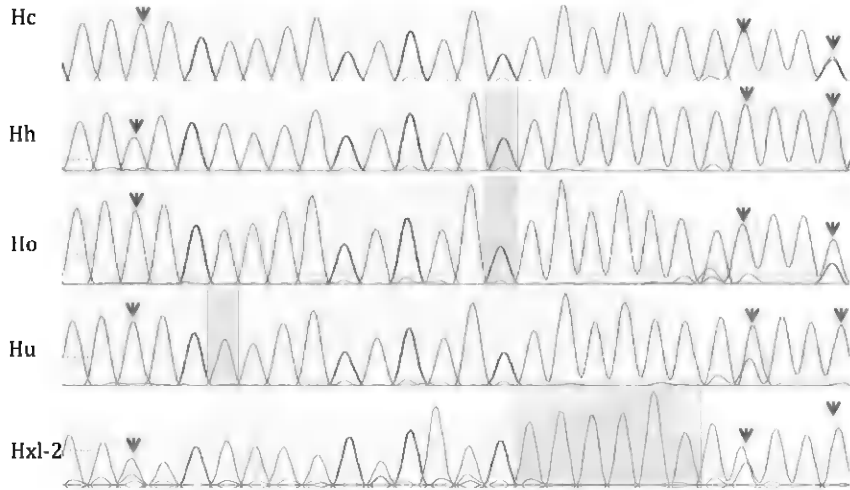
A. Sequence traces of four parental candidates and the hybrid. Arrows point to three positions, which show variations among the potential candidates. The hybrid Hxl-2 shows a combined trace for *H. heptaphyllus* and *H. umbellatus.* Hc, *H. chrysotrichus;* Hh, *H. heptaphyllus;* Ho, *H. ochraceus;* Hu, *H. umbellatus.*
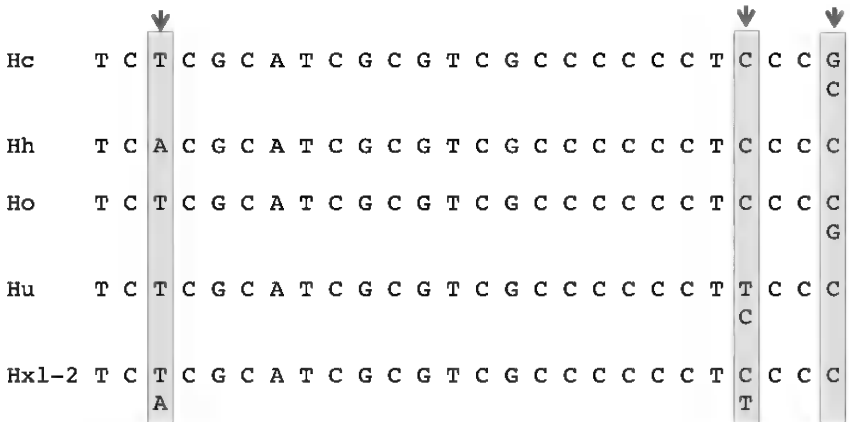
B. Translation of the traces to nucleotide sequences. Arrows point to the three positions identified in part A. The hybrid Hxl-2 shows a combined sequence for *H. heptaphyllus* and *H. umbellatus.* Hc, *H. chrysotrichus;* Hh, *H. heptaphyllus;* Ho. *H. ochraceus;* Hu, *H. umbellatus.*

Handroanthus ×lewisii Hodel, Henrich, Greby & Yansura, **nothosp. nov.** [*Handroanthus heptaphyllus* (Vell.) Mattos × *H. umbellatus* (Sond.) Mattos]. **TYPE: CULTIVATED. U.S.A. California.** Los Angeles County: Arcadia, Los Angeles County Arboretum and Botanic Garden, 7 Mar 2015, *1970-0966-S*1, J. Henrich & D.R. Hodel 627* (holotype: LASCA).

This new hybrid shares characters of both parents. In habit and branching structure it is more like *Handroanthus umbellatus*; in its glabrous or glabrescent leaves it is similar to both parents but the toothed leaflet margins are similar to those of *H. heptaphyllus*; in flower it is more like *H. umbellatus* initially with more yellow but aging to more like *H. heptaphyllus* with more pink or lavender, and in its mealy pubescent calyx is more similar to that of *H. heptaphyllus*; in its mostly glabrous fruit it is similar to both parents but lacks the strongly striate ridges of *H. heptaphyllus*. Table 1 and Figures 5 and 6 provide a comparison of characters of *Handroanthus ×lewisii* and its parents. Figures 5-18.

Tree, small to medium tree (Fig. 7), to ca. 15 m tall after 45 years but typically flowering when as small as 3-5 m tall. **Trunk** to ca. 30 cm DBH, typically with 2-3 strongly co-dominant leaders (Fig. 8); bark pebbly, grayish, tan in crevices between "pebbles" (Fig. 9); irregularly branched but typically scaffold branches regularly spaced and spreading horizontally to give "layered" look. **Leaves** palmately compound (Fig. 10), to ca. 23 × 19 cm, glossy green adaxially, paler abaxially, red-brown when young; petiole ca. 10 cm long, ca. 1.5 mm diam.; leaflets 5(-7), 2 or 3 paired lateral and one terminal); terminal leaflet with petiolule ca. 4.5 cm long, ca. 0.9 mm diam., leaflet blade to 10.5 × 4.5 cm, margins coarsely tooted in distal 4/5, 10 main lateral nerves on either side of midrib; distal lateral leaflets with petiolule to ca. 3 cm long, ca. 0.8 mm diam., leaflet blade 9 × 3 cm, margins coarsely toothed in distal 2/3; proximal lateral leaflets with petiolule to ca. 2 cm long, ca. 0.8 mm diam., leaflet blade to 6 × 2 cm, margins coarsely toothed in distal 2/3 (Fig. 10); petiole and petiolules grooved and +/- flattened adaxially, rounded abaxially, green, moderately to lightly covered with short, tan to whitish tomentum, all leaflets broadly lanceolate to oblong-elliptic, apex acute to acuminate, abruptly rounded, base cuneate, midrib abaxially with short, tan to whitish tomentum. **Inflorescence** a terminal, compact, vertically compressed, up to 16-flowered raceme to ca. 20 cm wide (Fig. 11). **Flowers** (Figs. 14-15) bisexual, zygomorphic, densely placed along a short rachis, paired or in threes, pedicels to 11 mm long, green, mealy pubescent. Calyx urn-shaped or campanulate, with gland pits toward distal end, to ca. 12 × 9 mm, green proximally, lavender distally, glabrous adaxially (inside), mealy pubescent with yellow-brown stellate hairs abaxially (outside), slightly angled longitudinally, 5-lobed, lobes ca. 5 mm long, swollen (saccate) , rounded to acute. Corolla ca. 8 × 6.5 cm, tubular or funnel-shaped, bi-laterally symmetrical (bilabiate), compressed to create horizontally open (oval-shaped) throat; 5-lobed, lobes ca. 2 × 2.5 cm, membranous, pale yellow, distal margin irregularly scalloped, erose, undulate; adaxially (inside) golden or dark yellow, on ventral surface with conspicuous, depressed, reddish brown or burgundy nerves and long, straight hairs, dorsal surface not so conspicuously nerved, abaxially (outside) with short, branched hairs on ventral surface and golden with slight suffusion of magenta, dorsal surface with heavy suffusion of magenta. Stamens 4, didynamous (2 long and 2 short), long to ca. 30 mm long, short to ca. 25 mm long; filaments slender, ca. 8 mm diam. at base and there adnate to corolla and with glandular hairs, ca. 0.5 mm diam. distally and glabrous; anthers ca. 7 mm long, divergent; staminode 1, to ca. 7 mm long. Pistil ca. 45 mm long; ovary ca. 7 × 1.2 mm, green, glabrous; style to ca. 35 mm long, ca. 0.7 mm diam., very light green; stigma flattened, ca. 2 × 1.5 mm, very pale yellow, eventually bi-lobed. Pistil with 5, laterally fused, quadrat nectary glands at base, these to ca. 2 × 1.5 mm. **Fruits** few (less than 20 per tree), to ca. 50 × 1 cm, cylindrical, green, glabrous (Fig. 12); seeds ca. 10-15 × 5-10 mm, thin, bialate, with hyaline-membranaceous wings clearly demarcated from the body, rarely fertile.

Figure 5. A comparison of inflorescences of *Handroanthus ×lewisii* (center, *1970-0966-S*1, J. Henrich & D. R. Hodel 627*, holotype) and its two parents, *H. umbellatus* (left, *1967-1455-P*3*) and *H. heptaphyllus* (right) at the Los Angeles County Arboretum and Botanic Garden (© D.R. Hodel).
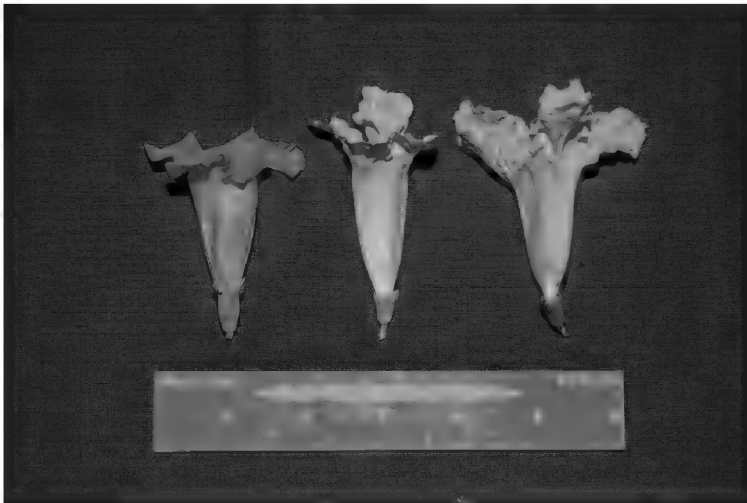

Figure 6. A comparison of flowers of *Handroanthus ×lewisii* (center, *1970-0966-S*1, J. Henrich & D. R. Hodel 627*, holotype) and its two parents, *H. umbellatus* (left, *1967-1455-P*3*) and *H. heptaphyllus* (right) at the Los Angeles County Arboretum and Botanic Garden (© D.R. Hodel).

Table 1. Comparison of *Handroanthus ×lewisii, H. heptaphyllus,* and *H. umbellatus.*

	H. heptaphyllus	*H. ×lewisii*	*H. umbellatus*
Leaflet shape.	Broadly lanceolate to ovate or oblong-elliptic.	Broadly lanceolate to oblong-elliptic.	Narrowly obovate to oblong-elliptic.
Leaflet margin.	Evenly serrate.	Evenly but coarsely toothed.	Entire.
Leaflet indumentum.	Lepidote abaxially and adaxially; pubescent with simple trichomes in axils of lateral nerves abaxially; or glabrescent.	Moderately to lightly covered with short, tan to whitish tomentum abaxially, glabrous adaxially; midnerve with short, tan to whitish tomentum abaxially; or glabrescent.	Lepidote abaxially and adaxially; stellate-rufescent abaxially and adaxially with few-branched trichomes along midnerve adaxially and in axils of lateral nerves adaxially; or glabrescent.
Inflorescence.	Terminal panicle.	Terminal, compact, vertically compressed, raceme.	Contracted, +/- fasiculate terminal cluster.
Flower color.	Magenta, throat yellow.	Yellow with suffusion of magenta; throat yellow.	Yellow.
Calyx.	Mealy pubescent with thick-stellate trichomes or glabrescent with lepidote scales.	Lightly mealy pubescent with yellow-brown stellate trichomes.	With sparse thick-stellate rufescent trichomes.
Fruit.	Glabrescent, strongly striate-ridged.	Glabrous, smooth.	Glabrous, smooth.

Figure 7. *Handroanthus ×lewisii* is typically a small to medium tree (Los Angeles County Arboretum and Botanic Garden) (© D.R. Hodel).

Figure 8. *Handroanthus ×lewisii* typically has two to three codominant leaders (Los Angeles County Arboretum and Botanic Garden) (© D.R. Hodel).

Figure 9. The bark of Handroanthus *×lewisii* is pebbly and grayish (Los Angeles County Arboretum and Botanic Garden) (© D.R. Hodel).

Figure 10. Leaves of *Handroanthus ×lewisii* are palmately compound with five to seven leaflets with coarsely toothed margins (© Los Angeles County Arboretum and Botanic Garden) (© D.R. Hodel).

Figure 11. Inflorescence of *Handroanthus ×lewisii* are a terminal, compact, vertically compressed, up to 16-flowered raceme to 20 cm wide (Los Angeles County Arboretum and Botanic Garden) (© D.R. Hodel).

Figure 12. Fruits of *Handroanthus ×lewisii* are few, cylindrical, green, and glabrous (Los Angeles County Arboretum and Botanic Garden) (© D.R. Hodel).

Additional specimens examined. CULTIVATED. USA. California. Los Angeles Co.: Arcadia, Los Angeles County Arboretum and Botanic Garden, *1970-0966-S*2, Henrich & Hodel 628* (LASCA,), *1970-0966-S*3, 629* (LASCA); Whittier, 9923 Colima Rd. (33°56'49.349"N, 118°00'29.005"W) *Henrich et al. 622* (LASCA), 10145 Colima Rd. (33°56'37.648"N, 118°00'37.919"W) *Henrich et al. 621* (LASCA.)

<center>DISCUSSION</center>

The epithet honors the late George Lewis, who first made the hybrid cross and who had a 33-year career with the Los Angeles County Arboretum and Botanic Garden, from 1957 to 1970, where he rose to the rank of senior gardener, and then later at Descanso Gardens, La Cañada Flintridge, from 1970 to 1990, where he rose to the rank of superintendent. We designate the cultivar name 'Apricot' and the common name apricot tab because they refer to the general color of the flowers and were originally coined by Arboretum staff.

The flower color of *Handroanthus ×lewisii* deserves a detailed discussion. When viewed from a distance the flowers appear to be apricot-colored, a light yellowish orange (Fig. 13). However, when viewed closely, individual colors contributed by each parent are clearly evident (Fig. 14). The adaxial or inside surface of the corolla is golden yellow, the color darkest proximally and lightest distally where the lobes are nearly membranous. The abaxial or outside surface of the corolla is golden yellow with a light suffusion of magenta on the ventral side and a heavy suffusion on the dorsal side. The suffusion of magenta on the dorsal side is heaviest or darkest proximally and lightest distally.

All of these flower colors transition as they age; generally the flowers open more yellow, more like *Handroanthus umbellatus*, and less magenta, less like *H. heptaphyllus*, then age to less yellow and more magenta. The yellow fades adaxially nearly to white and abaxially to whitish or ivory with irregular tinges of magenta. The yellow actually masks the magenta; fading away it leaves or reveals the magenta base, intensifying the magenta. Once fallen on the ground, the magenta intensifies even more. Also, one's distance and angle from the tree, angle of the sun, and one's position relative to the sun tend to influence flower color.

Three trees from Lewis's original 1970 cross are extant at the Los Angeles County Arboretum and Botanic Garden. Located at the top of Tallac Knoll, the three are about 20 feet apart in a line and are accessioned as *1970-0966-S*1* (Fig. 16), *1970-0966-S*2*, and *1970-0966-S*3*, respectively north to south. Similar in habit, size, and flowers, they are about 15 m tall; have trunks 42.9 cm (25.9 + 17.0), 29.9 cm, and 24.3 cm DBH, respectively; and bloom in February and March. Also, at least eight of the grafted apricot tabs are planted elsewhere at the Arboretum, and several more were distributed through Arboretum plant sales and as gifts to other botanical gardens. Notable trees are at the South Coast Botanic Garden in Palos Verdes Peninsula and on Colima Road south of Whittier Blvd. in Whittier (Figs. 17-18), both in Los Angeles County; the home of plant enthusiast Brent Wigand in Wildomar, Riverside County; and several other private gardens. Most of these grafted plants are in the same or similar age/size class, are about 5 m tall and wide and have trunks 10 to 15 cm DBH.

Others have made this hybrid in recent years. Eric Schmidt (pers. com.) of Harry P. Leu Gardens in Orlando, Florida notes that Bernie Peterson of Rockledge Gardens in Cocoa, Florida has made several hybrids involving various combinations of *Handroanthus chrysotrichus*, *H. heptaphyllus*, *H. impetiginosus*, and *H. umbellatus*. One of the hybrids made was perhaps *H. ×lewisii*.

Figure 13. When viewed from a distance the flowers of *Handroanthus ×lewisii* appear to be apricot colored, a light yellowish orange (Los Angeles County Arboretum and Botanic Garden, *1970-0966-S*1, J. Henrich & D.R. Hodel 627*, holotype) (© D.R. Hodel).

Figure 14. When viewed closely, individual colors contributed by each parent are clearly evident in flowers of *Handroanthus ×lewisii* (Los Angeles County Arboretum and Botanic Garden, *1970-0966-S*1, J. Henrich & D.R. Hodel 627*, holotype) (© D.R. Hodel).
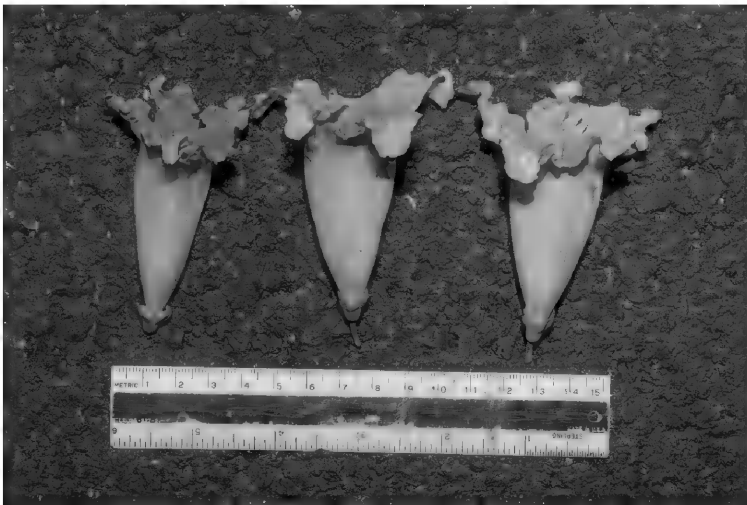
Figure 15. Flowers of *Handroanthus ×lewisii* are bisexual, zygomorphic, densely placed along a short rachis, and yellow with suffusion of magenta (Los Angeles County Arboretum and Botanic Garden) (© D.R. Hodel).

Figure 16. Marianne Hodel (foreground) and coauthor James E. Henrich provide scale for one of the three trees of *Handroanthus ×lewisii* from Lewis's original 1970 cross (Los Angeles County Arboretum and Botanic Garden, *1970-0966-S*1, *Henrich & Hodel 627*, holotype) (© D.R. Hodel).

Figure 17. The more northerly tree of *Handroanthus ×lewisii* at 9923 Colima Road in Whittier is likely from Lewis's original 1970 cross (*J. Henrich et al. 622*) (© D.R. Hodel).

CULTIVATION AND MANAGEMENT

The apricot tab does not readily produce fruits, which is advantageous for those managing this tree in the landscape. Managers have to contend with little fruit and seed litter and no seedlings appearing as weeds. In contrast, *Handroanthus heptaphyllus* and *H. umbellatus*, especially the former, produce abundant fruits that are rather unattractive when persisting on the tree and liberate great quantities of seeds, many of which germinate in the landscape and become weeds.

The apricot tab is readily propagated by grafting. Mary Foote, the Arboretum's plant nursery manager in the 1980s and early 1990s, successfully grafted it, using *Handroanthus heptaphyllus* as the root stock. Scion wood was from one or more of the original three extant trees on Tallac Knoll but which particular tree or trees were not always specified. Current nursery manager Sherry Tobin used the cleft graft technique to propagate the Apricot Tab successfully on to seedling-grown *H. heptaphyllus*. The apricot tab can also likely be propagated from semi-hardwood tip cuttings made after flowering and prior to growth flushing; the use of rooting hormone, bottom heat, overhead mist, and high light would probably yield the best results. Air layering is another possible method to propagate the apricot tab. However, plants grafted on to seedlings might develop a deeper, well structured root system that would provide better anchorage and support than cutting-grown or air-layered trees. This situation has occurred in Hawaii with the rainbow shower (*Cassia × nealiae* H.A. Irwin & Barneby), where grafting was recommended over air layering because of its stronger root system (Hickok 1954). Indeed, seedlings of *H. heptaphyllus* typically develop a rather deep, central taproot from which other roots then arise, and they are unusually difficult to pull out of the garden as weeds.

Figure 18.   The more northerly tree of *Handroanthus ×lewisii* at 9923 Colima Road in Whittier has exceedingly handsome flowers in their brightness, intensity, purity, and demarcation of the magenta and yellow colors (*J. Henrich et al. 622*) (© D.R. Hodel).

Little training and pruning are necessary to achieve a well structured apricot tab because it tends to grow upright with several strong leaders and layers of horizontal branches radially and vertically well spaced along the trunk.   However, if necessary, prune and train to a central leader, subordinating lateral branches until the desired height is attained, and a handsome, well structured tree will result.

Pests, diseases, and nutritional disorders are unknown for the apricot tab in the landscape in southern California.   Providing proper cultivation, including planting, mulch, and judicious irrigation, will preclude most problems.   The most limiting factor in their cultivation might be cold, but the apricot tab has tolerated temperatures to about -6 C for short periods at night with little or no damage and has recovered with damage from even colder temperatures.   Based on the distribution and ecology of its parents and their performance in southern California, the apricot tab could probably be classified as a low water user and, once well established in the landscape, would likely require deep irrigation (to 30 cm deep) only one to two times a month in the summer and much less frequently at other times, especially if there is sufficient rain.   Indeed, the two trees in Whittier, in a paved-over median with 75 cm cutouts, apparently receive little or no irrigation and at the end of nearly four years of severe drought are still performing adequately if not outstandingly; thus, like many other woody trees and shrubs, the apricot tab likely needs only about 30 to 40% of reference evapotranspiration for the site (ETo) once well established.

ACKNOWLEDGEMENTS

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A MULTIVARIATE STUDY OF *SOLIDAGO* SUBSECT. *TRIPLINERVIVAE* IN WESTERN NORTH AMERICA: THE *SOLIDAGO LEPIDA* COMPLEX (ASTERACEAE: ASTEREAE)

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ABSTRACT

Solidago subsect. *Triplinerviae* includes four species native to western North America: *S. altissima, S. elongata, S. gigantea,* and *S. lepida.* All of these except *S. gigantea* have been included at one time or another within *S. canadensis.* While rather similar among themselves, each species is distinguished by different sets of indument, leaf, and inflorescence traits. A series of multivariate morphometric analyses were performed on 244 specimens to discover additional technical traits useful in separating the species and to elucidate problems with identification in a group of species complicated by multiple ploidy levels and considerable infraspecific variation. Statistical support for recognizing *S. gigantea* var. *shinnersii* and *S. lepida* var. *salebrosa* was generated in comparisons of the varieties with the typical variety in each species.

Solidago subsect. *Triplinerviae* (Torrey & A. Gray) Nesom (Asteraceae: Astereae) includes 17 species native North and South America (Semple 2017 frequently updated). Semple and Cook (2006) recognized 11 species with infraspecific taxa in several species occurring in Canada and the USA: *S. altiplanities* Taylor & Taylor, *S. altissima* L., *S. canadensis* L., *S. elongata* Nutt., *S. gigantea* Ait., *S. juliae* Nesom, *S. leavenworthii* Torrey & A. Gray, *S. lepida* DC., *S. rupestris* Raf., *S. shortii* Torrey & A. Gray, and *S. tortifolia* Ell. Semple (2013) and Semple et al. (2013) added two additional species, *S. brendiae* Semple and *S. fallax* (Fern.) Semple, based on a multivariate study of the *S. canadensis/S. lepida* complex in eastern North America with *S. elongata* included for comparison. Data on type specimens of names critical in this study are presented in Table 1.

Semple et al. (2015) presented a multivariate morphometric analysis of *Solidago altissima, S. canadensis,* and similar species. Lopez Laphitz and Semple (2015) included some species native to the southern USA and Mexico in a study of the *S. chilensis* Meyen/*S. microglossa* DC. complex native to South America. Semple et al. (2016) and Semple and Lopez Laphitz (2016) included *S. durangensis* Nesom and *S. pringlei* Fern. native to Mexico in multivariate studies determining their morphological affinities within the genus *Solidago* and in subsect. *Triplinerviae.* Taxonomic problems involving species of subsect. *Triplinerviae* native to the western provinces in Canada and the western states of the USA were not fully addressed in these previous studies.

Over many years, Cronquist advocated lumping all western species of subsect. *Triplinerviae* except *Solidago gigantea* into *S. canadensis* (e.g., Cronquist 1955, 1994; Hitchcock & Cronquist 1973). In the Flora of British Columbia, Douglas (1998) lumped *S. altissima* var. *gilvocanescens* (Rydb.) Semple, *S. canadensis, S. elongata,* and *S. lepida* into a single very broadly defined *S. canadensis* but recognized *S. gigantea* as separate and left local botanists with keys insufficient to clarify which species of subsect. *Triplinerviae* were present in the province. Email exchanges between the first author and Frank Lomer regarding the identification of multiple *Solidago* collections in British Columbia indicated the need for additional work on the *Triplinerviae* problem in the Pacific Northwest by the Astereae Lab. Discussions with the late John K. Morton, who made numerous *Solidago* collections with Joan Venn (deposited in TRT, WAT, and other herbaria) over multiple

Table 1. Basionyms and types of taxa included in this study.

Solidago canadensis L., Sp. Pl. 878. 1753. **TYPE**: "Hab. Virginia, Canada", Herb. Linn. 998.2 (LINN!; Lectotype [A. Gray, 1882]). *Kalm s.n.*, Herb. Linn. 998.3 (LINN!) is pinned to 998.2; it is *S. rugosa* Mill. var. *rugosa*. Herb. Linn. 998.6 (LINN!) is *S. canadensis* var. *canadensis*.

Solidago canadensis L. var. *gilvocanescens* Rydb. Contr. U.S. Nat. Herb. 3: 162. 1895. **TYPE**: USA. Nebraska. Hooker Co.: Cody's Lakes at the head of the Dismal R, sandy soil, 10 Aug 1893, *Rydberg 1662* (holotype: US, photo!; isotype: GH!, NY2, photos!).

Solidago elongata Nutt., Trans. Amer. Philos. Soc., n. ser. 7: 327. 1840. Nom. cons., Semple (2007), non Pépin (1834), nec Hort. Par. ex A. Gray (1884). **TYPE**: {USA. Oregon. Sauvie Island W of Ft. Vancouver, Washington,} Wappatoo Island and Columbia Plains, [Sep 1834, or Aug-Sep 1835,] *Nuttall s.n.* (lectotype designated by (Semple 2007): BM!; isolectotype: PH!, S). "Wapp.", [Sep 1834, or Aug-Sep 1835] *Nuttall s.n.* (probable isolectotype: GH!).

Solidago gigantea Ait., Hort. Kew. 3: 211. 1789. **TYPE**: "Nat. North America. Cult. 1758, by Mr. Philip Miller." Hort. Kewensis 1778 {back of sheet} (holotype: BM!)

Solidago lepida DC., Prodr. 5: 339. 1836. **TYPE**: "ad Mullgrave seu Nootka," {USA. Alaska: Mulgrave, Nootka Sound, Yakutat Bay}, *Haenke s.n.* (holotype: G-DC!). The type has broadly oblanceolate coarsely serrate leaves.

Solidago lepida var. β *subserrata* DC., Prodr. 5: 339. 1836. **TYPE**: USA. Alaska. "Ad Mullgrave sen Nootka", {Mulgrave, Nootka Sound, Yakutat Bay}, *Haenke s.n.* (holotype: G-DC!). The type has oblanceolate finely serrate leaves.

Solidago pruinosa Greene, Pittonia 4: 70. 1899. **SYNTYPES**: CANADA. Saskatchewan. Moose Jaw, Assiniboia, 13 Aug 1895, *Macoun 10893* (holotype: ND-G digital image! marked at "type" by Greene; isotype: CAN!). *Macoun 10894* (ND-G digital image!, incorrectly designated in Semple et al. 2015 as lectotype).

Solidago serotina Ait., Hort. Kew. 3: 211. 1789. Non Retzius (1781), nec Hook. (1835). **TYPE**: "Nat. of North America. Cult. 1758, by Mr. Philip Miller" (holotype: BM!).

Solidago serotina Ait. var. *salebrosa* Piper in Piper & Beattie, Fl. Palouse Region, 185. 1901. **TYPE**: USA. Washington. Pullman, *Piper 1580* (holotype: WS!; isotype: GH!).

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decades focusing on subsect. *Triplinerviae*, confirmed the first author's field observations that hexaploid plants of *S. gigantea* and *S. lepida*, and particularly var. *salebrosa* (Piper) Semple, could be very difficult to distinguish along the northern edge of the prairies from Alberta to Manitoba and along streams and rivers in eastern Washington and northern Idaho. Both *S. gigantea* and *S. lepida* var. *salebrosa* were left out of the multivariate analyses presented in Semple et al. (2013) in the paper on the *S. canadensis/S. lepida* complex in eastern North America.

Solidago altissima var. *gilvocanescens* is the only morph of the species present in western Canada and the western USA and is distinguished by being mostly diploid and tetraploid and having short canescent stems from base to apex and having upper strigose stem leaves that are sometimes more serrate than found in var. *altissima* and var. *pluricephala* M.C. Johnston (Semple et al. 2015). Variety *gilvocanescens* is common across the prairies west to the Rocky Mountains. In Montana, the mountains are broken up by broad valleys across much of the state where the Rocky Mts. cut northwest. In the first edition of the Flora of Alberta, Moss (1959) used the synonym *S. pruinosa* Greene with *S. canadensis* var. *gilvocanescens* Rydb. listed as a synonym. In the Flora of the Pacific Northwest, Hitchcock and Cronquist (1973) listed the taxon as *S. canadensis* var. *gilvocanescens*, as did Scoggan (1979) in the Flora of Canada, Moss revised by Packer (1983) in the second edition of the Flora of Alberta, and Douglas et al. (1998), who noted the variety as being present in the interior of British Columbia, but Douglas et al. (2002) did not map the distribution. The variety was illustrated in Semple et al. (2015). *Solidago canadensis* is not native to western Canada and the western USA as the species was defined in Semple and Cook (2006) and Semple et al. (2013), although var. *canadensis* has been listed as present in some floras, e.g., Moss revised by Packer (1983).

Solidago elongata is distinguished by being mostly diploid, having stems that are usually very sparsely hairy proximally and more so distally, having club shaped rather than secund conical inflorescences, and having very few small stipitate glands on the bracts, peduncles, and phyllaries in the inflorescence (Figs. 1-3). Every species of *Solidago* can have some small stipitate glands in the inflorescence, but only a few are obviously densely glandular. *Solidago elongata* was treated as *Solidago lepida* var. *elongata* (Nutt.) Fern., but Fernald (1915) applied the combination to plants in both western and eastern North America. Hitchcock and Cronquist (1973) treated *S. elongata* as a synonym of *S. canadensis* var. *salebrosa* (Piper) M.E. Jones as did Scoggan (1979) and Cronquist (1994). *Solidago elongata* was treated as *S. canadensis* subsp. *elongata* (Nutt.) D.D. Keck by Semple (1993), who later (Semple 2012) treated it as *S. elongata* in the second edition of the Jepson Manual.

Solidago gigantea is usually the least glandular and least pubescent species of subsect. *Triplinerviae* in North America (Figs 4-7). Stems can be glaucous and or often anthocyanotic. The stem leaves are usually sharply serrate from lower stem to the inflorescence. The inflorescence is secund conical and the longer lower branches are usually strongly arching; overall the inflorescence is less densely branched than *S. altissima*, *S. canadensis*, and *S. elongata*. Moss (1959), Hitchcock and Cronquist (1973), and Douglas et al. (1983) recognized the species as present in Alberta, the Pacific Northwest, and British Columba, respectively. Semple (1993) listed *S. gigantea* as present in California but rejected this identification in Semple (2012) and treated the California plants as *S. lepida* var. *salebrosa*. *Solidago gigantea* is diploid and tetraploid in eastern North America but is exclusively hexaploid on the prairies. The latter cytotype has been treated as *S. gigantea* var. *shinnersii* Beaudry and *Solidago shinnersii* (Beaudry) Beaudry, but these names were treated as synonyms of *S. gigantea* in Semple and Cook (2006) following G. Morton (1984). As a consequence of the results presented below, Semple (2017, frequently updated) added var. *shinnersii* to the list of taxa that should be recognized in *Solidago*.

Solidago lepida is the most morphologically varied of the western species of subsect. *Triplinerviae* (Figs. 8-13). Stem height is highly variable depending upon latitude and growing conditions. Stems vary from glabrous from base to apex to glabrous below to moderately densely short-woolly canescent distally to sparsely to moderately short-woolly canescent proximally to distally. Leaves can be narrowly lanceolate to broadly lanceolate and entire or finely to coarsely serrate; leaves vary from glabrous to sparsely strigose to moderately strigose. Upper stem leaves are usually much less reduced in size into the inflorescence in var. *lepida*, while upper stem leaves of var. *salebrosa* tend to be reduced below the inflorescence. Inflorescences vary from narrowly club-shaped to leafy secund conical forms with short spreading lower branches in var. *lepida* to broadly secund conical in var. *salebrosa* with intermediate forms common. In his flora of the Rocky Mountains, Rydberg (1922) treated var. *salebrosa* as *S. salebrosa* (Piper) Rydb. Moss (1959) recognized *S. lepida* and briefly discussed var. *fallax* Fern. and var. *elongata*. Hitchcock and Cronquist (1973) treated *S. lepida* as a synonym of *S. canadensis* var. *subserrata* (DC.) Cronquist. Moss revised by Packer (1983) included *S. lepida* in *S. canadensis* in a broadly defined var. *canadensis*. Douglas et al. (1998) noted that *S. lepida* equaled *S. canadensis* var. *subserrata* in their treatment and had outer phyllaries about half the length of the inner, while in *S. canadensis* var. *salebrosa* the phyllaries more graduated. Cronquist (1994) proposed the combination *S. canadensis* var. *lepida* (DC.) Cronquist in the list of synonyms under *S. canadensis*, noting that "the holotype at G! approaches the *elongata* phase of var. *salebrosa* in its inflorescences." The species includes diploids, tetraploids, and hexaploids, which results in considerable variation in head size; phyllaries are generally graduated but sometimes the outer phyllaries are closer to half the length of the inner. Stipitate glands are often difficult to see on diploids but are larger and more obvious on hexaploids, which are the most stipitate glandular in subsect. *Triplinerviae*. Glands are can be found on upper stem leaves, leaves in the inflorescence, bracts, peduncles, and phyllary margins or outer faces, and sometimes on all these structures or only some of them.

Figure 1. Morphology of *Solidago elongata*: *Semple & Brouillet 7114* (WAT) from Clatsop Co., Oregon.
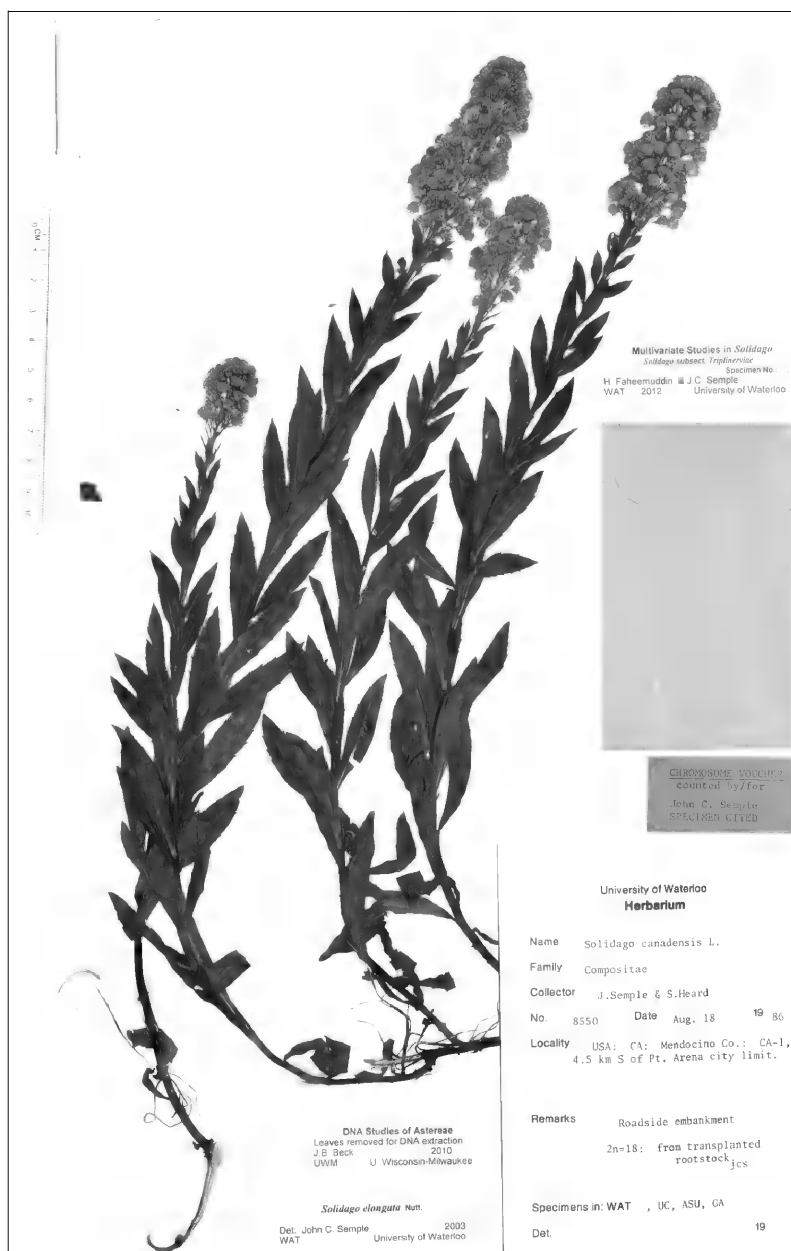
Figure 2. Morphology of *Solidago elongata*: *Semple & Heard 8550* (WAT) from Mendocino Co., California.

Figure 3. Details of *Solidago elongata*. **A-B.** Lower and mid stems; *Semple & Heard 8786* (WAT); California. **C.** Mid stem and leaf base; *Semple & Heard 8537* (WAT); California. **D.** Mid stem leaf; *Semple & Brouillet 7132* (WAT), Oregon. **E.** Small inflorescence; *Semple & Heard 8786* (WAT). **F.** Heads; *F. Lomer 6361*(WAT), British Columbia. Scale bars = 1 mm in A-C, F; = 1 cm in D-E.
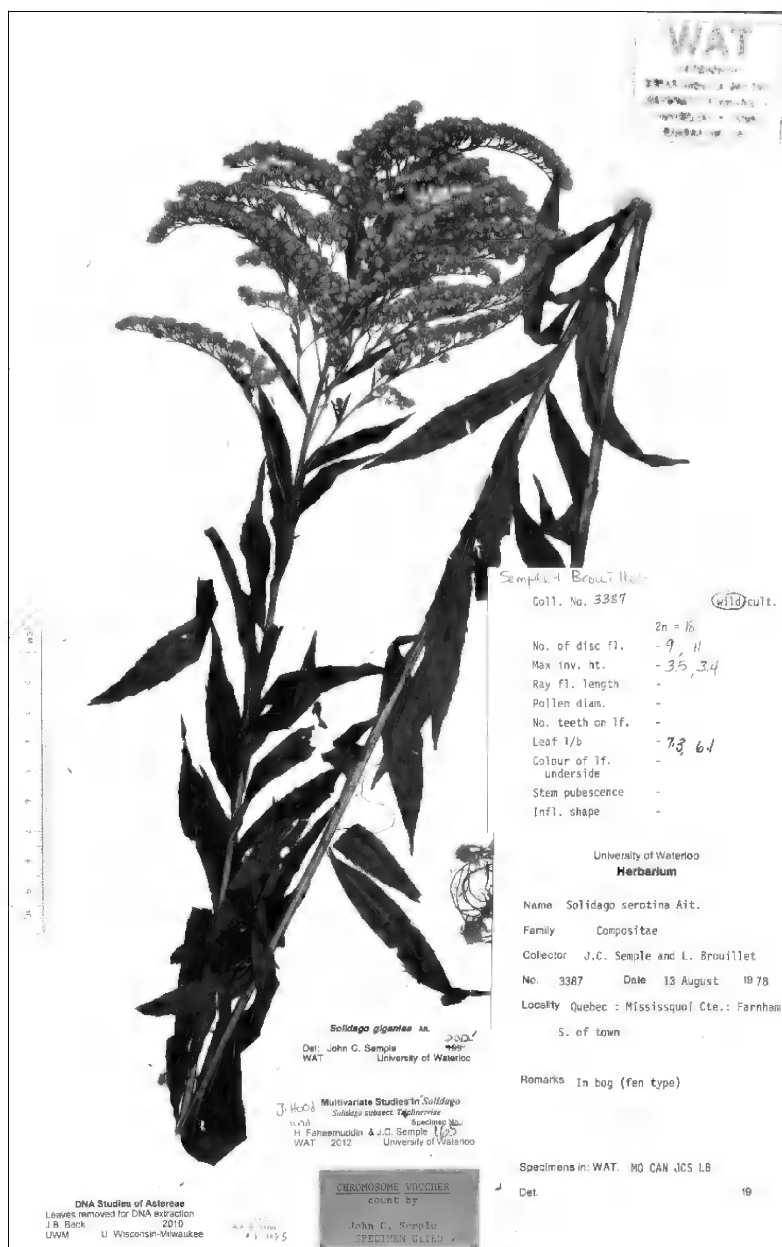
Figure 4. Morphology of *Solidago gigantea*: *Semple & Brouillet 3387* (WAT), Farnham, Québec, $2n$=18.
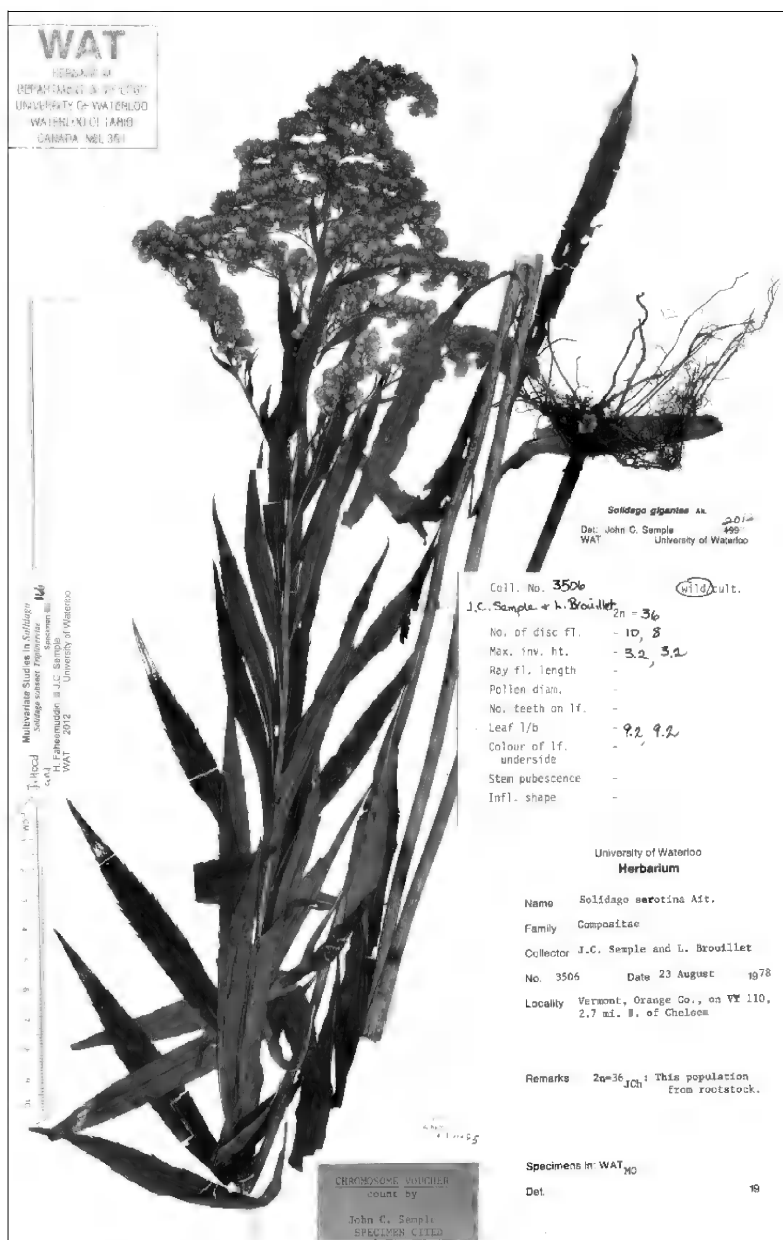
Figure 5. Morphology of *Solidago gigantea*: *Semple & Brouillet 3506* (WAT), Chelsea, Vermont, 2*n*=36.
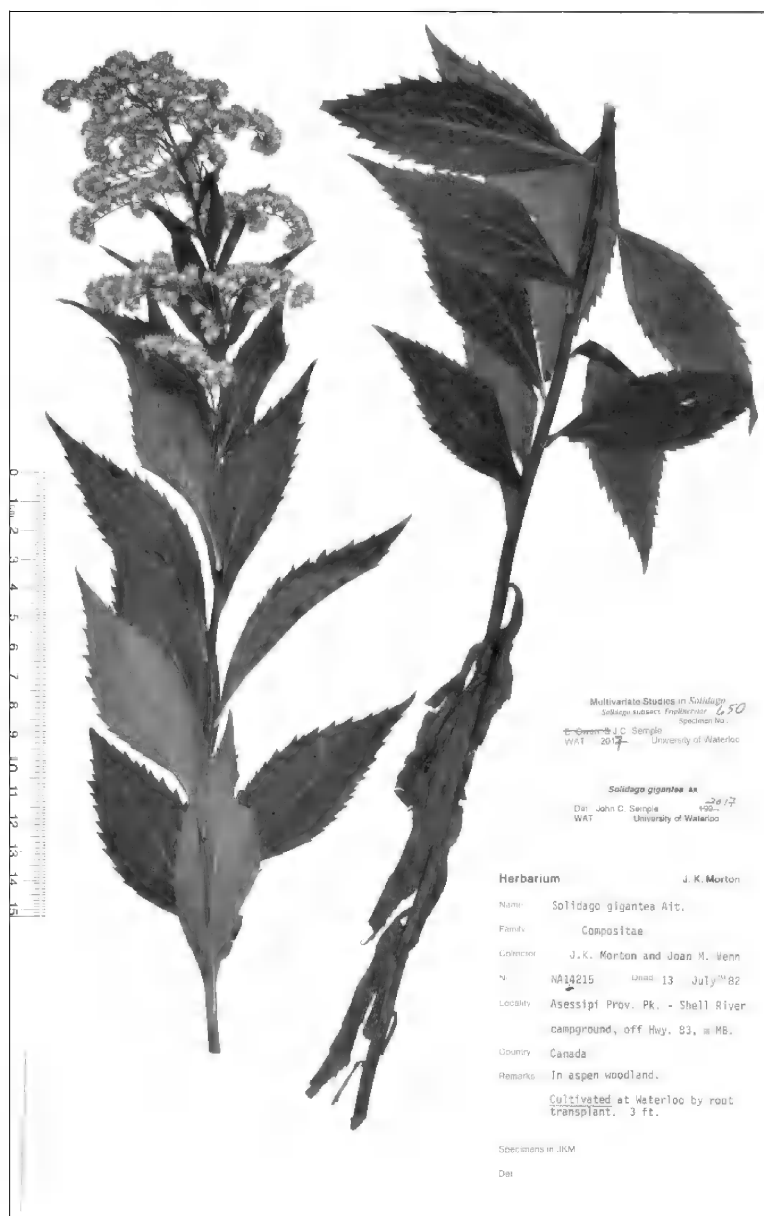
Figure 6. Morphology of *Solidago gigantea*, broader leaf morph: *Morton & Venn NA14215* (TRT), Asessipi Provincial Park, Manitoba, 2n=54.
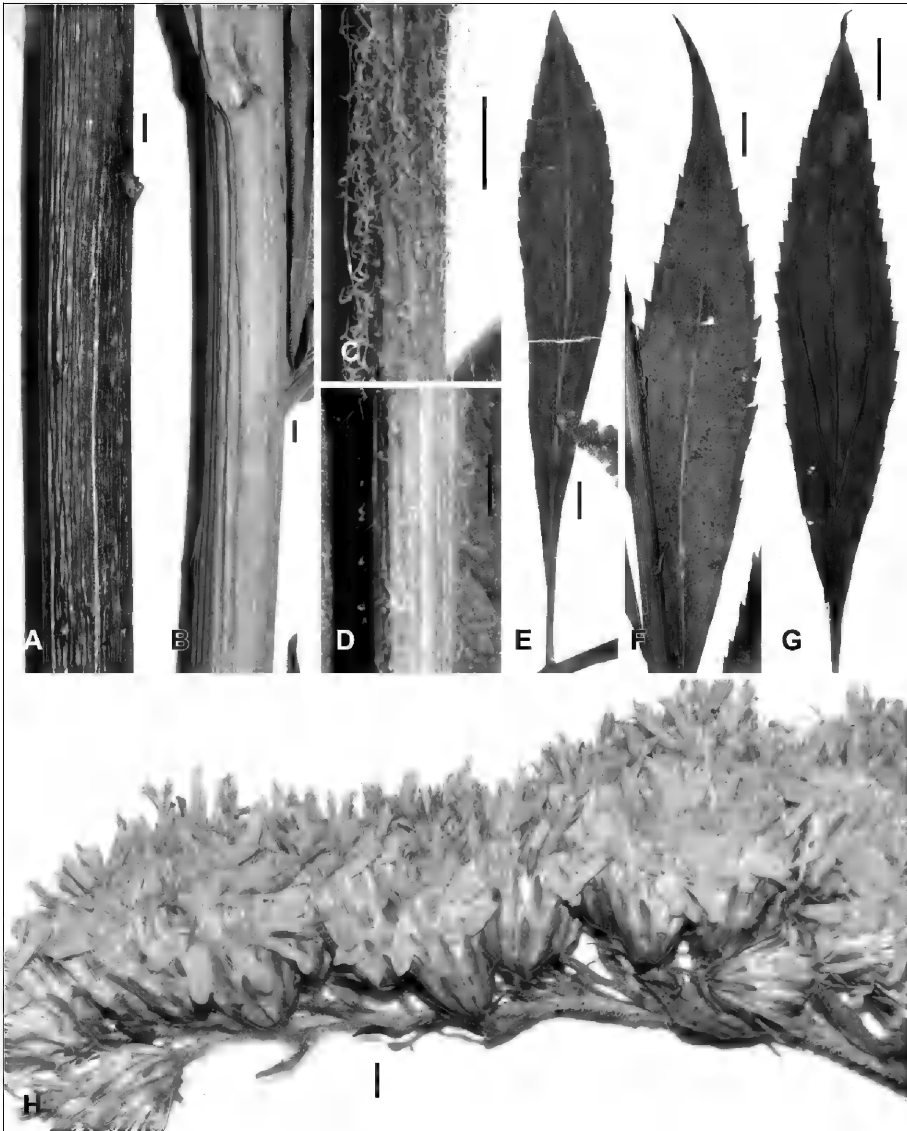
Figure 7. Details of *Solidago gigantea*. **A.** Lower stem; *Semple & B. Semple 11489* (WAT); New Brunswick. **B.** Mid stem; *Semple & Brouillet 4507* (WAT); Iowa. **C-D.** Upper and lower stem in inflorescence; *J.K. Morton NA18725* (TRT); Illinois. **E.** Lower stem leaf; *J.K. Morton NA18688* (TRT), cult. greenhouse, transplanted from Pennsylvania. **F.** Mid stem leaf; *J.K. Morton NA18764* (TRT), North Carolina. **G.** Mid stem leaf; *J.K. Morton NA18772* (TRT), North Carolina. **H.** Heads; *J.K. Morton NA18764* (TRT), 2*n*=36. Scale bars = 1 mm in A-D, H; = 1 cm in E-G.
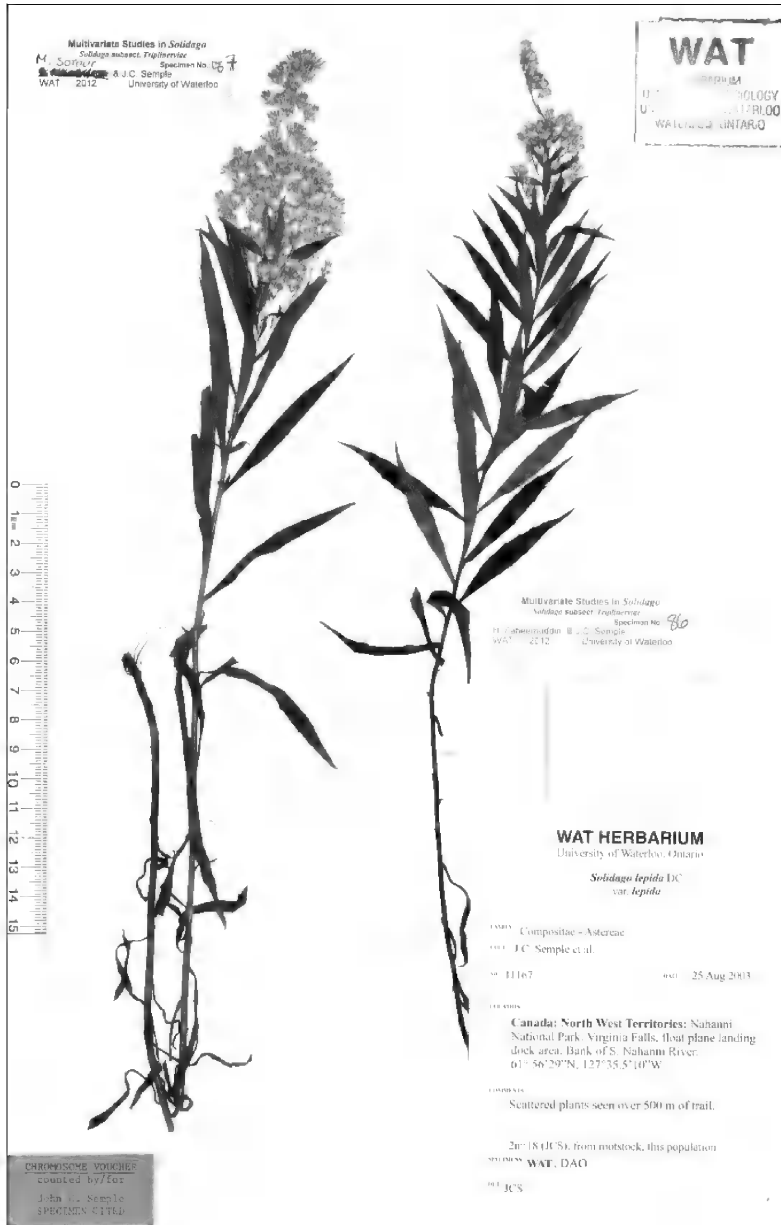
Figure 8. Morphology of *Solidago lepida* var. *lepida*: *Semple et al. 11167* (WAT), Nahanni Nat. Park. Reserve, Northwest Territories, 2*n*=18.

Figure 9. Morphology of *Solidago lepida* var. *lepida*: *Chmielewski et al. CC4736* (WAT), S of Dease Lake, British Columbia, 2*n*=36; shoot on right side has damaged inflorescence with elongated branches.

Figure 10. Morphology of *Solidago lepida* var. *lepida*: *Morton & Venn NA17568* (TRT), Gaspé Penisula, Québec, 2*n*=54.
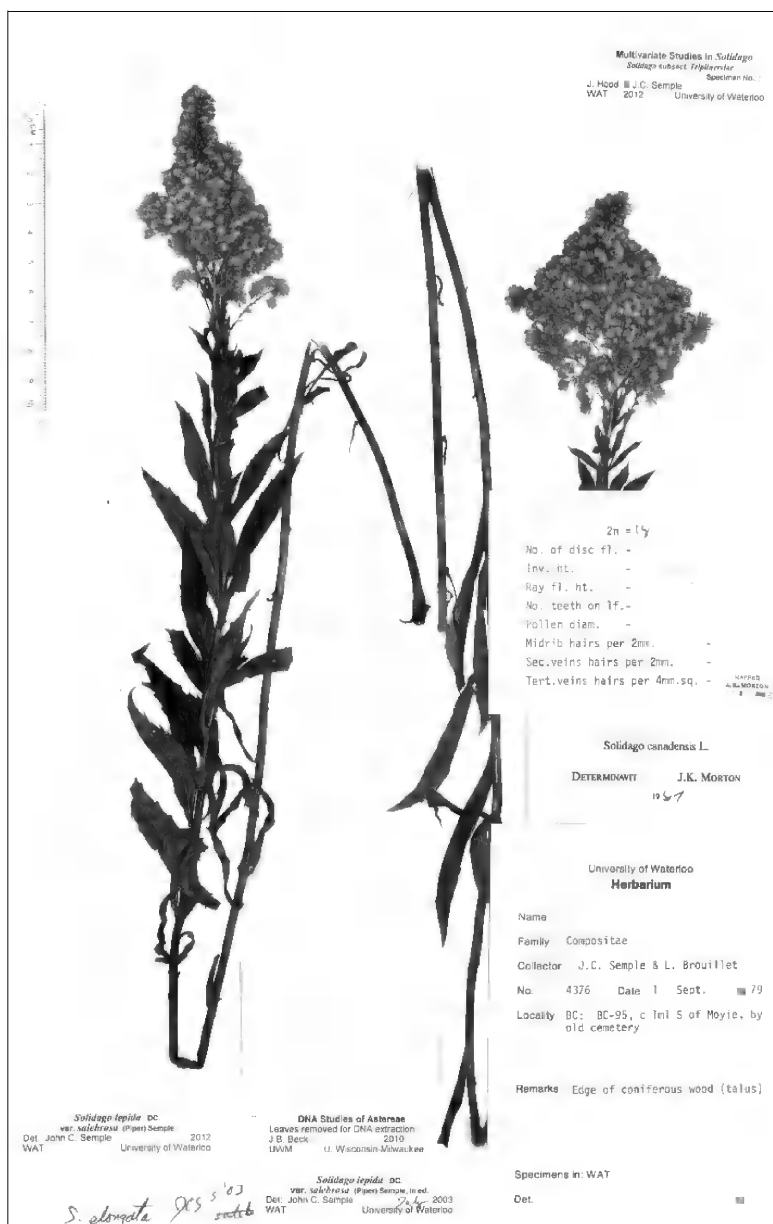
Figure 11. Morphology of *Solidago lepida var. salebrosa* diploid from west slope of Rocky Mts.: *Semple & Brouillet 4376* (WAT), Moyie, British Columbia; an *S. elongata*-like morphotype.

Figure 12.   Morphology of *Solidago lepida var. salebrosa*: *Semple & Xiang 10324* (WAT), Edith Lake, Belt Mts., Montana, *2n*=54; *S. gigantea*-like but moderately to densely stipitate glandular in inflorescence.
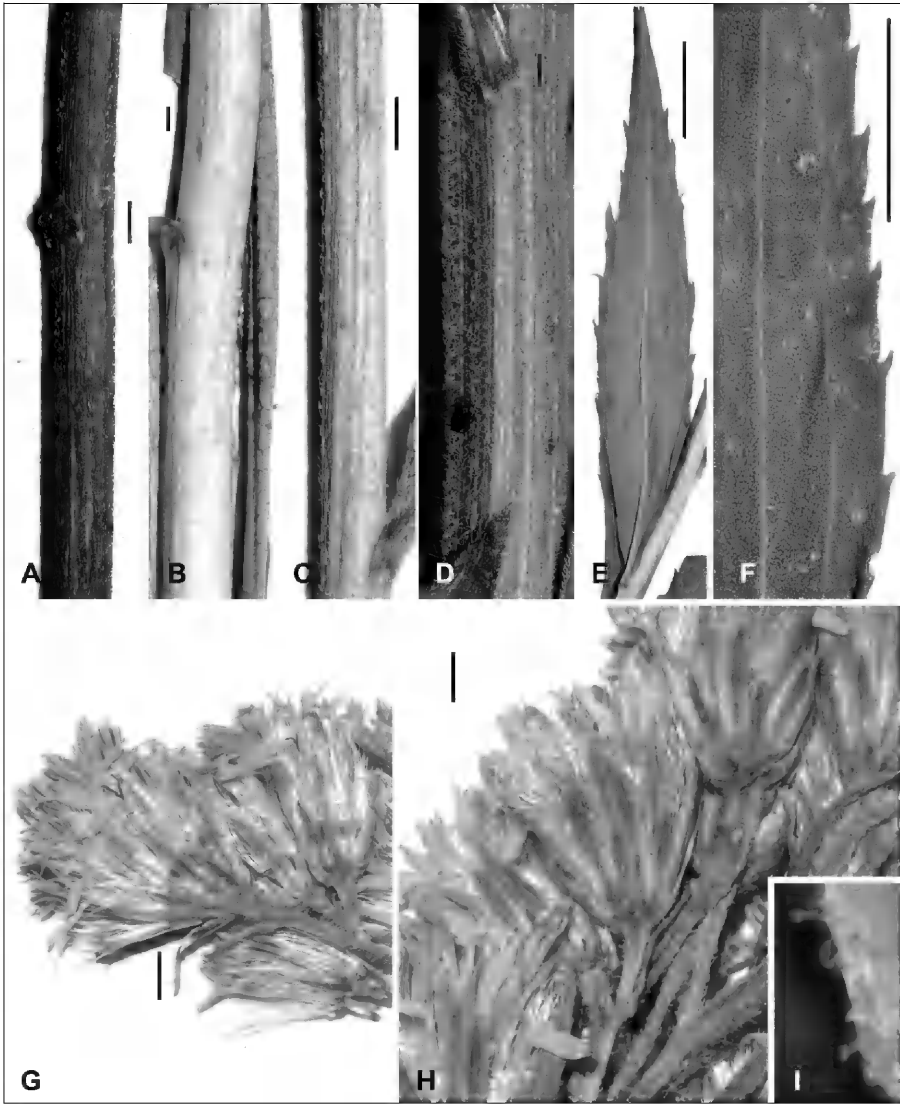
Figure 13. Details of *Solidago lepida*. **A-B.** Lower stems. **A.** *Semple 11167* (WAT); Northwest Territories. **B.** *Semple et al. 9207* (WAT), Wyoming. **C.** Mid stem; *Semple 11376* (WAT), Idaho. D. Upper stem; *Oldham 30688* (WAT), Ontario. **E.** Mid stem leaf; *Semple et al. 9209* (WAT), Wyoming. **F.** Mid stem leaf margin; *Semple & Cli-Marchaud 11173* (WAT), Northwest Territories. **G.** Heads; *Semple 11167* (WAT); 2*n*=18. **H.** Heads; *Semple et al.* (WAT), Utah; 2*n*=54. **I.** Glands on phyllary; *Morton & Venn NA17568* (TRT); Québec. Scale bars = 1 mm in A-D, G-H; = 1 cm in E-F.   A, C, D, F, H-I = var. *lepida*; B, E, G = var. *salebrosa.*

Each species has a significant portion of its range allopatric from the other species, but ranges overlap on the margins. *Solidago altissima* var. *gilvocanescens* is common on the prairies from central Alberta to New Mexico and extends east to Manitoba south to northern Texas. The range extends eastward in the Prairie Peninsula in Illinois and Indiana. It also occurs in a few valleys west of the front range of the Rocky Mts. in southeastern and southcentral British Columbia. *Solidago elongata* is confined to the coastal ranges and the Cascade Mts. from southwestern British Columbia to the coastal ranges and the Sierra Nevadas in California (Fig. 14). Diploid and tetraploid *Solidago gigantea* occur in moist soils along streams and rivers and in thickets from Nova Scotia to eastern Manitoba south to Panhandle Florida and eastern Texas (Fig. 15). Hexaploids occur in similar habitats on the prairies from Manitoba to Alberta and south to Colorado and Texas. *Solidago lepida* occurs on tundra and in boreal and pine forests from Central Alaska and the eastern Aleutian Islands south to Arizona and northeastern Mexico and east in the boreal forests and aspen parklands to Ontario with scattered and possibly introduced populations in eastern Québec and New Brunswick (Fig. 16). Diploids, tetraploids and hexaploids occur in the western part of the range, while only hexaploids are known in Ontario and eastward. The var. *lepida* occurs throughout the range of the species though less common in the southern part of the Rocky Mts., while var. *salebrosa* occurs throughout the mountainous parts of the range. Some var. *salebrosa* like plants occur in the southern edge of the aspen parkland/boreal forest in Alberta, Saskatchewan, and Manitoba but these may be hybrids between hexaploid var. *lepida* and hexaploid *S. gigantea*.

Figure 14. Range of distribution of *Solidago elongata* and locations of specimens included in the analyses; British Columbia south to California.
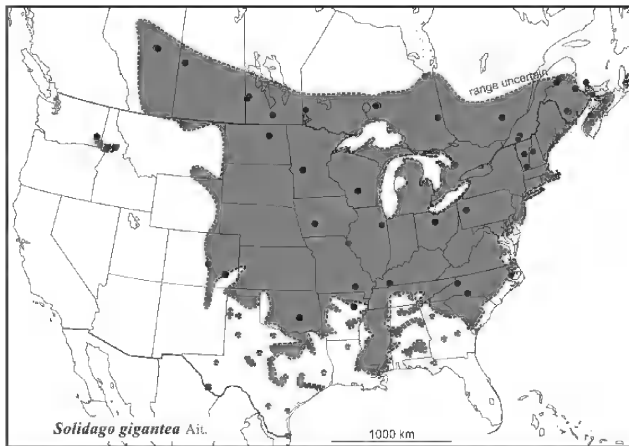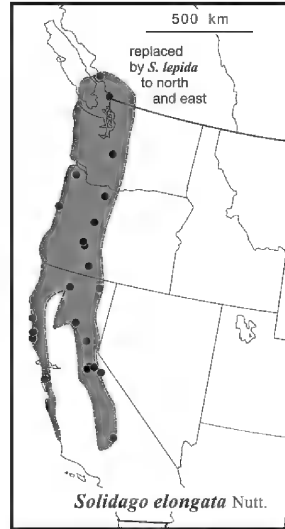
Figure 15. Range of distribution of *Solidago gigantea* and locations of specimens included in the analyses.
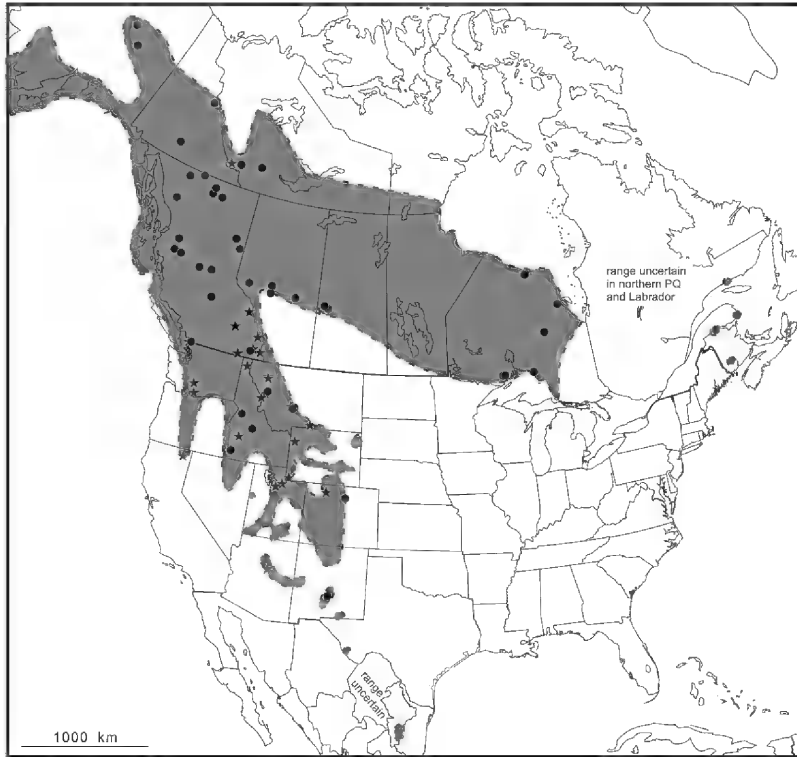
Figure 16. Range of distribution of *Solidago lepida* and locations of specimens included in the analyses; var. *lepida* (dots), var. *salebrosa* (stars).

A multivariate analysis focusing on western North American *Solidago* subsect. *Triplinerviae* has not been previously published. A number of problems need exploration. Does typical *S. canadensis* occur in the Pacific Northwest? How distinct are *S. elongata* and *S. lepida*? Is *S. gigantea* always easily distinguished from *S. lepida*? Should *S. lepida* be divided into var. *lepida* and var. *salebrosa* based on differences in inflorescence branching pattern? Are the diploid plants on the western slope of the Rocky Mts. members of *S. elongata* or *S. lepida*? Are the western hexaploid prairie individuals of *S. gigantea* sufficiently distinct from the diploid/tetraploid eastern individuals to warrant recognition as var. *shinnersii*? The following analyses and results were undertaken to answer these questions.

MATERIALS AND METHODS

In total, 244 specimens from the J.K. Morton personal herbarium now deposited in TRT, NH, UBC, and WAT in MT (Thiers, continuously updated) were scored and included in the analyses: *S. altissima* var. *gilvocanescens* (33 specimens, most were included in Semple et al. 2015), *S. canadensis* (53 specimens; included in Semple et al. 2015; all from eastern North America), *S. elongata* (28 specimens, most included in Semple et al. 2013), *S. gigantea* (49 specimens), and *S.*

lepida (81 specimens; 50 specimens of var. *lepida* with most included in Semple et al. 2013 and 31 specimens of var. *salebrosa*). These were selected from more than 3500 specimens examined in many herbaria. For each specimen, 13 vegetative and 16 floral traits were scored when possible: 1-5 replicates per character depending upon availability of material and whether or not the trait was meristic (Table 1). Basal rosette leaves were not present. Lower stem leaves were sometimes not present. Mean values were used in the analyses, while raw values were used to generate ranges of variation for each trait. All traits scored are listed in Table 2. Leaf size in the inflorescence, orientation and density of the lower inflorescence branches, and density of stipitate glands were used in assigning specimens to a priori groups and were not included in the multivariate analyses.

Table 2. Traits scored for the multivariate analyses of 244 specimens of *Solidago* subsect. *Triplinerviae*.

Abbreviation	Description of trait scored
STEMHT	Stem height measured from the stem base to tip (cm)
LLFLN	Lower leaf length measured from the leaf base to tip (mm)
LLFWD	Lower leaf width measured at the widest point (mm)
LLFWTOE	Lower leaf measured from the widest point to the end (mm)
LLFSER	Lower leaf dentation–number of serrations of lower leaf
MLFLN	Mid leaf length measured from the leaf base to tip (mm)
MLFWD	Mid leaf width measured at the widest point (mm)
MLFWTOE	Mid leaf measured from the widest point to the end (mm)
MLFSER	Mid leaf dentation–number of serrations of mid leaf
ULFLN	Upper leaf length measured form the leaf base to tip (mm)
ULFWD	Upper leaf width measured at the widest point (mm)
ULFWTOE	Upper leaf measured from the widest point to the end (mm)
ULFSER	Upper leaf dentation–number of serrations of upper leaf
CAPL	Length of inflorescence (cm)
CAPW	Width of inflorescence (cm)
CAPBRLN	Length of longest inflorescence branches (cm)
INVOLHT	Involucre height (mm)
OPHYLN	Outer phyllary length (mm)
IPHYLN	Inner phyllary length (mm)
IPHYLW	Inner phyllary width (mm; not measures on the majority of specimens)
RAYNUM	Number of ray florets per head
RLAMLN	Ray strap length top of the corolla tube to the tip of the strap (mm)
RLAMPWD	Ray strap width measured at the widest point (mm)
RACHLN	Ray floret cypsela body length at anthesis (mm)
RPAPLN	Ray floret pappus length at anthesis (mm)
DCORLN	Disc floret corolla length from the base to tip of the corolla lobes (mm)
DLOBLN	Disc floret corolla lobe length lobe (mm)
DACHLN	Disc floret achene length at anthesis (mm)
DPAPLN	Disc floret pappus length at anthesis (mm)

All analyses were performed using SYSTAT v.10 (SPSS 2000). Details on the methodology were presented in Semple et al. (2015) and are not repeated here. Six STEPWISE discriminant analyses were performed. In the first analysis, *S. altissima* var. *gilvocanescens*, *S. canadensis*, *S. elongata*, S. *gigantea*, and *S. lepida* were included. In the second analysis, *S. elongata*, *S. gigantea*, and *S. lepida* were included. In the third analysis, *S. elongata* and *S. lepida* were included. In the fourth analysis, *S. gigantea* and *S. lepida* were included. In the fifth analysis, *S. lepida* var. *lepida* and var. *salebrosa* were included. In the six analysis, *S. gigantea* var. *gigantea* and var. *shinnersii* were included.

Many of the specimens included in the analyses had their chromosome number determined, but only some have been published, often under incorrect names. These will all be published or corrected in a set of manuscripts now in preparation reporting chromosome numbers and the cytogeography of *S. altissima*, *S. canadensis*, *S. elongata*, *S. gigantea* and *S. lepida* by the Astereae lab or in collaboration with the J.K. Morton lab. Only ploidy levels are referred to below; details of locations will be included in these manuscripts in preparation.

RESULTS
Five species level a priori groups analysis

The Pearson correlation matrix yielded r > |0.7| for the following pairs of leaf traits reducing the number to be used: 1) mid stem leaf length and upper stem leaf length, 2) mid stem leaf width and upper stem leaf width, 3) number of mid stem leaf margin serrations and number of upper stem leaf margin serrations, 4) ray floret ovary body length at anthesis and disc floret ovary body length at anthesis, 5) ray floret pappus length and disc floret corolla length, 6) ray floret pappus length and disc floret pappus length, and 7) disc floret corolla length and disc floret pappus length. Lower leaves were usually absent and lower leaf traits were excluded from discriminant analyses. Inflorescence length and width traits were highly variable in all species and were not included in the analyses. Length of leaves in the inflorescence and the degree of arching of the lower branches of an inflorescence and the branch density of the inflorescence were used in assigning specimens to an priori group. For example, specimens of *S. gigantea* typically had broad inflorescences with arching lower branches and overall had the least densely branched inflorescences. The density of stipitate glands were used in assigning specimens to an a priori group. Usually glands were obvious and abundant on either bracts, peduncles and/or phyllaries of specimens of *S. lepida*. Such glands were usually obscure or present in very low numbers in other species. Less glandular specimens of *S. lepida* were sometimes difficult to assign to the *S. lepida* a priori group; these were usually diploid when the ploidy level was known. The size of leaf serrations varied considerably even within a species and on a single shoot. In all species, lower mid stem leaves usually had the largest serrations in the greatest numbers, while upper stem leaves usually had serrations reduced in size and number.

In the STEPWISE discriminant analysis 244 specimens of five species level a priori groups (*Solidago altissima*, *S. canadensis*, *S. elongata*, *S. gigantea*, and *S. lepida*), the following six traits were selected as best separating the groups and are listed in order of decreasing F-to-remove values: ray floret pappus length at anthesis (31.44), number of mid stem leaf serrations (20.26), mid stem leaf width (13.29), number of disc florets (9.82), number of ray florets (6.41), and disc corolla lobe length (5.95). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 3. F-values based on Mahalanobis distances between group centroids indicated the largest separations were between *S. canadensis* and *S. lepida* (56.513), *S. canadensis* and *S. gigantea* (42.847), and *S. canadensis* and *S. elongata* (33.979), and the least separations were *S. elongata* and *S. lepida* (11.267) and *S. altissima* (var. *gilvocanescens*) and *S. elongata* (11.840).

Table 3. Between groups F-matrix for the five a priori group analysis (df = 6   225).

Group	altissima gilvocanescens	canadensis	elongata	gigantea
canadensis	19.840			
elongata	11.840	33.979		
gigantea	22.931	42.847	20.087	
lepida	13.475	56.513	11.367	17.188

Wilks' lambda = 0.15003 df = 6 4 230; Approx. F= 23.6681 df = 24 786 prob = 0.0000

In the Classificatory Discriminant Analysis of the five species level a priori groups (*Solidago altissima*, *S. canadensis*, *S. elongata*, *S. gigantea*, and *S. lepida*), percents of correct a posterori assignment to the same a priori group ranged from 89% down to 53%. The Classification matrix and Jackknife classification matrix are presented in Table 4. Results are presented in order of decreasing percents of correct placement. Forty-seven of the 53 specimens of the *S. canadensis* a priori group (89%) were assigned a posteriori to the *S. canadensis* group; 26 specimens with 91-100% probability, 7 specimens with 80-88%, 7 specimens with 70-79%, 3 specimens with 60-68%, 2 specimens with 56-57% probability, and 1 specimen with 47% probability (24% to *S. altissima*, 13% to *S. gigantea* and 11% to *S. lepida*). Six specimens of the *S. canadensis* a priori group were assigned a posteriori to other species: 3 specimens to *S. altissima* with 83% probability (*Semple & Brouillet 2786* WAT from Bruce Co., Ontario; var. *hargeri*), 63% probability (*Semple 9087* WAT from Winnebago Co., Wisconsin; var. *hargeri*), and 52% probability (37% to *S. canadensis*; *Morton & Venn NA10785* WAT from Bruce Co., Ontario; var. *canadensis*); 2 specimens to *S. elongata* with 78% probability (*Morton & Venn NA17617* TRT from Washington Co., Maine) and 44% probability (*Morton & Venn NA8219* WAT from Bruce Co., Ontario; var. *canadensis*); and 1 specimen to *S. gigantea* with 35% probability (26% to S. altissima, 25% to *S. canadensis*, and 9% to *S. elongata*; *Melville 401* WAT from Timiskaming Dist., Ontario). Twenty-two of 28 specimens of *S. elongata* (79%) were assigned a posteriori to the *S. elongata* group: 8 specimens with 90-96% probability, 4 specimens with 83-89% probability, 3 specimens with 74-76% probability, 4 specimens with 51-58% probability, and 2 specimens with 45% probability (44% to *S. lepida*; *Semple & Brouillet 7125* WAT from Lincoln Co., Oregon), and 44% probability (28% to *S. gigantea* and 26% to *S. lepida*; *Lomer 6466* WAT from Surrey, British Columbia). Six specimens of the *S. elongata* a priori group were assigned a posteriori to other species groups: 4 specimens to *S. altissima* with 66% probability (*Wells 699* UBC from Tsawwassen, British Columbia), 45% probability (35% *S. elongata* and 18% *S. lepida*; *Semple & Heard 8543* WAT from Medocino Co., California; glabrous lower stem, mid stem moderately short woolly), 39% probability (29% each to *S. elongata* and *S. lepida*; *Semple & Heard 8660* WAT from Tulare Co., California), and 35% probability (29% to *S. lepida*, 23% to *S. elongata* and 13% to *S. gigantea*; *Semple & Brouillet 7114* WAT from Clatsop Co., Oregon; lower stem glabrous, Fig. 1); 1 specimen to *S. canadensis* with 62% probability (19% to *S. altissima* and 17% to *S. elongata*; *Semple & Heard 8492* WAT from San Mateo Co., California); and 1 specimen to *S. lepida* with 56% probability (43% to *S. elongata*; *Semple & Brouillet 7170B* WAT from Lane Co., Oregon; small narrowly lanceolate entire leaves; 2*x*). Thirty-six of the 48 specimens of the *S. gigantea* a priori group (75%) were assigned a posteriori to the *S. gigantea* group: 13 specimens with 90-100% probability, 9 specimens with 80-88% probability, 4 specimens with 73-79% probability, 5 specimens with 61-69% probability, 2 specimens with 55% probability (16% to *S. altissima*, 15% to *S. elongata*, and 6% to *S. lepida*; *Semple & Keir 4693* WAT from Loggieville, New Brunswick), and 51%

Table 4. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of five a priori groups; a posteriori placements to groups in rows.

Group	altissima	canadensis	elongata	gigantea	lepida	% correct
altissima	23	3	4	1	1	72
canadensis	3	47	2	1	0	89
elongata	4	1	22	0	1	79
gigantea	2	2	3	36	5	75
lepida	13	0	13	9	39	53
Totals	45	53	44	47	46	71

Jackknifed classification matrix

Group	altissima	canadensis	elongata	gigantea	lepida	% correct
altissima	23	3	4	1	1	72
canadensis	3	47	2	1	0	89
elongata	4	1	21	0	2	75
gigantea	2	2	3	36	5	75
lepida	14	0	14	9	37	50
Totals	46	53	44	47	45	70

probability (40% to *S. lepida*; *Melville 984* WAT from Thunder Bay Dist., Ontario; typical *S. gigantea* inflorescence), and 3 specimens with 43% (31% to *S. lepida* and 16% to *S. altissima*; *Semple & B. Semple 6178* WAT from Ingolf, Kenora Dist., Ontario; 6*x*), 42% probability (33% to *S. lepida* and 19% to *S. elongata*; *Semple 11517* WAT from Fredericton, New Brunswick; 4*x*), and 41% probability (23% to *S. altissima*, 16% to *S. lepida*, and 11% to *S. elongata*; Turner 3205 WAT from Fort Saskatchewan, Alberta). Twelve specimens of the *S. gigantea* a priori group plus for additional specimens included a posteriori were assigned a posteriori to other species: 8 specimens to *S. lepida* with 85-41% probability; 3 specimens to *S. elongata* with 90%, 68%, and 67% probabilities; 3 specimens to *S. altissima* with 49% probability (26% to *S. elongata* and 17% to *S. canadensis*; *Semple & B. Semple 11489* WAT from Cape Jourimain, New Brunswick), 47% probability (40% to *S. lepida*; *Semple 11523* WAT from York Co., New Brunswick), and 30% probability (25% to *S. gigantea*, 23% to *S. lepida* and 21% *S. elongata*; Melville 974 WAT from Thunder Bay Dist., Ontario; 4*x*); and 2 specimens to *S. canadensis* with 52% probability (33% to *S. gigantea*; *Semple et al. 3422* WAT from Rougemont, Québec) and 42% probability (28% to *S. gigantea* and 20% to *S. lepida*; *Semple & Brouillet 6984* WAT from Douglas Co., Minnesota; 6*x*). Twenty-three of 32 specimens of the *S. altissima* var. *gilvocanescens* a priori group (72%) were assigned a posteriori to the *S. altissima* group: 2 specimens with 92% and 96% probabilities, 7 specimens with 80-89% probability, 2 specimens with 76% and 78% probabilities, 1 specimen with 67% probability, and 4 specimens with 59% probability (16% to *S. canadensis* and 15% to *S. elongata*; *Morton & Venn NA15663* TRT from Mower Co., Minnesota; 4*x*), 57% probability (41% to *Morton & Venn NA16028* TRT from Scott Co., Iowa; 2*x*) 56% probability (41% to *S. canadensis*; *Semple et al. 9210* WAT from Carbon Co., Wyoming; 4*x*), and 49% probability (31% to *S. elongata*; *Morton & Venn NA15672* from Rock Co., Iowa; 4*x*). Nine specimens of the *S. altissima* var. *gilvocanescens* a priori group were assigned to other species: 4 specimens to *S. elongata* with 63% probability (19% to *S. altissima* and 11% to *S. lepida*; *Semple & B. Semple 11389* WAT from Glacier Co., Montana; 4*x*), 48% probability (39% to *S. altissima*; *Semple & B. Semple 10645* WAT from Ste. Agathe, Manitoba; 2*x*), 44% probability (34% to *S. altissima*; *Morton & Venn NA16303* from Canadian Co., Oklahoma), and 37% probability (30% *S. altissima* and 32% *S. lepida*; *Semple et al. 9208* WAT from Carbon Co.,

Wyoming; 4*x*); 3 specimens were assigned to *S. canadensis* with 82% probability (6% each to *S. bicolor*; 66), 79% probability (22% to *S. roanensis*; 77), and 76% probability (36% to *S. roanensis*; 66); 1 specimen to *S. gigantea* with 72% probability (20% to *S. lepida*; *Cannings s.n.* UBC from Penticton, British Columbia; 33 cm tall shoot with indument typical of var. *gilvocanescens* but large leaves for size of plant); and 1 specimen to *S. lepida* 53% probability (22% to *S. elongata* and 21% to *S. altissima*; *Semple & K. Shea 1926* WAT from Balgonie, Saskatchewan; indument of var. *gilvocanescens*). Thirty-nine of 74 specimens of the *S. lepida* a priori group (53%) plus 5 additional specimens added a posteriori were assigned a posteriori to the *S. lepida* group: 6 specimens with 91-96% probability, 8 specimens with 80-89% probability, 4 specimens with 71-78% probability, 10 specimens with 61-69% probability, 6 specimens with 50-58% probability, and 4 specimens with 48% probability (32% to *S. gigantea* and 19% to *S. altissima*; *Semple & B. Semple 5817* WAT from Boulder Co., Colorado; 6*x*), 48% probability (*Semple & Brouillet 7209* WAT from Teton Co., Wyoming; 6*x*), 44% probability (38% to *S. altissima* and 14% to *S. canadensis*; *Oldham & Sutherland 24798* WAT from Polar Bear Prov. Park, Ontario), and 36% probability (34% to *S. altissima* and 18% to *S. elongata*; *Ringius et al. 940* WAT from Kapiskau R. near James Bay, Kenora Dist., Ontario). Thirty-four specimens of the *S. lepida* a priori group plus 1 specimen added a posteriori were assigned a posteriori to other species: 14 specimens were assigned to *S. altissima* var. *gilvocanescens* with 49-80% probability (none had the stem indument of var. *gilvocanescens*); 13 specimens were assigned to *S. elongata* with 40-80% probability; 9 specimens were assigned to *S. gigantea* with 40-91% probability.

Two dimensional plots of CAN1 versus CAN3 and CAN1 versus CAN2 canonical scores for 244 specimens of *Solidago altissima* var. *gilvocanescens*, *S. canadensis*, *S. elongata*, *S. gigantea*, and *S. lepida* are presented in Fig. 17. Eigenvalues on the first three axes were 1.688, 0.682 and 0.284.

Three species level a priori groups analysis

The Pearson correlation matrix yielded r > |0.7| for the following pairs of leaf traits reducing the number to be used: mid stem leaf length and upper stem leaf length, number of mid stem leaf margin serrations and number of upper stem leaf margin serrations, and ray floret ovary body length at anthesis and disc floret ovary body length at anthesis. Mid stem leaf length, number of upper stem leaf margin serrations, and disc floret ovary body length at anthesis were included in the analysis.

In the STEPWISE discriminant analysis of 150 specimens of three species level a priori groups (*Solidago elongata*, *S. gigantea*, and *S. lepida*), the following seven traits were selected as best separating the groups and are listed in order of decreasing F-to-remove values: number of upper stem leaf margin serrations (33.01), mid stem leaf length (22.15), disc corolla lobe length (10.26), involucre height (7.39), number of ray florets (5.57), disc corolla length (4.48), and ray floret lamina length (4.26). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 5. F-values based on Mahalanobis distances between group centroids indicated the largest separation was between *S. elongata* and *S. gigantea* (21.892), and the least separations were between *S. gigantea* and *S. lepida* (12.862) and *S. elongata* and *S. lepida* (13.818).

In the Classificatory Discriminant Analysis of 150 specimens of the three species level a priori groups (*Solidago elongata*, *S. gigantea*, and *S. lepida*), percents of correct a posterori assignment to the same a priori group ranged from 68-100%. The Classification matrix and Jackknife classification matrix are presented in Table 6. Results are presented in order of decreasing percents of correct placement. All 28 specimens of the *S. elongata* a priori group
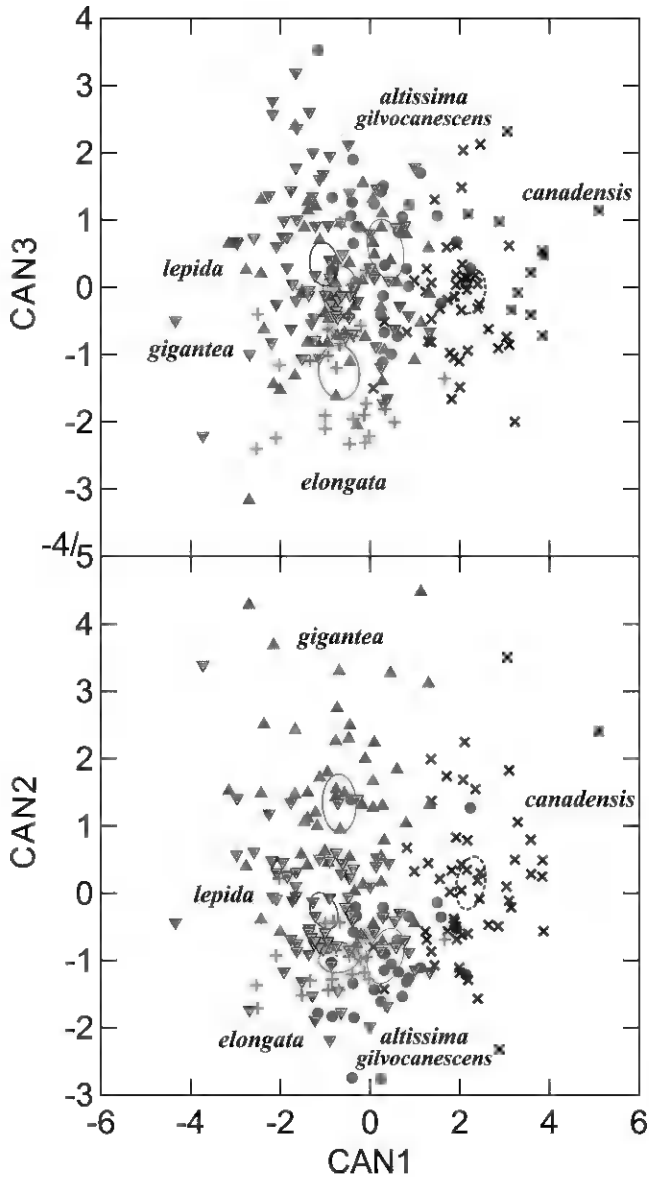
Figure 17. Two dimension plots of CAN1 versus CAN2 and CAN1 versus CAN3 scores generated by the Canonical Analysis of 244 specimens of *Solidago altissima* var. *gilvocanescens* (red dots), *S. canadensis* (×s), *S. elongata* (+s), *S. gigantea* (blue triangles), and S. *lepida* (inverted yellow triangles); 95% confidence ellipses are shown for each taxon.

Table 5. Between groups F-matrix for the five a priori groups analysis (df = 7   141).

Group	elongata	gigantea
gigantea	21.892	
lepida	13.818	12.862

Wilks' lambda = 0.3309 df = 7 2 147; Approx. F= 14.8734   df = 14   282 prob = 0.0000

Table 6. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of three a priori groups; a posteriori placements to groups in rows.

Group	elongata	gigantea	lepida	% correct
elongata	28	0	0	100
gigantea	3	36	9	75
lepida	11	13	50	68
Totals	42	49	59	76

Jackknifed classification matrix

Group	elongata	gigantea	lepida	% correct
elongata	26	0	2	93
gigantea	4	36	8	75
lepida	12	14	48	65
Totals	42	50	58	73

 (100%) were assigned a posteriori into the *S. elongata* group; 14 specimens with 92-99% probability, 4 specimen with 80-85% probability, 2specimens with 72% and 79% probabilities, 7 specimens with 60-68% probability (including *Semple & Brouillet 7114* WAT), and 1 specimen with 49% probability (49% to *S. lepida*; *Wells 699* UBC from Tsawwassen, British Columbia).   Thirty-six of the 48 specimens of the *S. gigantea* a priori group (75%) plus 7 additional specimens included a posteriori were assigned a posteriori to the *S. gigantea* group; 21 specimens with 90-100% probability, 7 specimens with 81-89% probability, 6 specimens with 72-76% probability, 1 specimens with 67% probability, and 2 specimen with 59% probability (*Semple & Brouillet 4507* TRT from Adair Co., Iowa; tall shoot with glabrous stem, lanceolate leaves, and a large open secund conical inflorescence with long diverging lower branches; 6*x*) and 57% probability (195).   Twelve specimens of the *S. gigantea* a priori group were assigned to other species: 12 specimens to *S. lepida* with 83% probability (*Morton & Venn NA17577* TRT from Gaspé Penisula, Québec; open secund conical inflorescence with some glands; 4*x*), 81% probability (*Semple & B. Semple 11489* WAT from Cape Jourimain, New Brunswick; small leafy inflorescence with short diverging lower branches; 2*x*), 72% probability (*Morton & Venn NA14185* TRT from Maidstone, Saskatchewan; broadly oblanceolate mid stem leaves to lanceolate upper stem leaves; 6*x*), 63% probability (*Semple & B. Semple 6718* WAT from Ingolf, Kenora Dist., Ontario; leaves are lanceolate; 6*x*), 59% probability (*Cheek 1987* NH from KwalZulu-Natal South Africa; typical looking *S. gigantea*, not glandular), 56% probability (*Semple & Brouillet 7292* WAT from Bent Co., Colorado; leaves are lanceolate to narrowly lanceolate; 6*x*), 56% probability (*Morton NA18706* TRT from Crawford Co., Ohio; narrow lanceolate leaves with few small margin serrations, not glandular; 4*x*), 55% probability (*Morton & Venn NA17597* TRT Gaspé Penisula, Québec; open elongated secund conical inflorescence with some glands; 4*x*), 53% probability (*Semple & Brammall 2743* WAT from Hughes Co., Oklahoma; narrow

lanceolate leaves, open leafy inflorescence with diverging lower branches, glands on peduncles, bracts and phyllaries; 6*x*), and 35% probability (*Semple & Brouillet 4173* WAT from Bagot, Manitoba; broad oblanceolate to lanceolate leaves, open secund conical infloresence; 6*x*); and 3 specimens to *S. elongata* with 94% probability (*Semple & B. Semple 11489* WAT from Cape Jourimain, New Brunswick; small leafy inflorescence with short diverging lower branches; 2*x*; first of two shoots of this collection), 91% probability (*Semple & B. Semple 11489* WAT from Cape Jourimain, New Brunswick 2*x*; second of two shoots of this collection), and 88% probability (*Morton & Venn NA14213* TRT from Roblin, Manitoba; treated as *S. gigantea* but subsequently annotated as *S. lepida* aff. var. *lepida*; ascending diverging lower inflorescence branches, glandular; 6*x*). Fifty of the 74 specimens of the *S. lepida* a priori group (68%) plus 6 additional specimens added a posteriori were assigned a posteriori to the *S. lepida* group: 12 specimens with 92-100% probability, 7 specimens with 83-89% probability, 7 specimens with 70-79% probability, 12 specimen with 60-68% probability, and 7 specimens with 59% probability (*Bell & Davidson 27* UBC from Fernie, British Columbia; var. *salebrosa*; lanceolate leaves reduced distally, secund conical inflorescence, heads with small involucres with some glands), 59% probability (*Semple & B. Semple 5817* WAT from Boulder Co., Colorado; 6*x*), 57% probability (*Semple & B. Semple 11367* WAT from Custer Co., Idaho; var. *lepida*; 2*x*), 53% probability (*Semple & Brouillet 7066* WAT from Valley Co., Idaho; var. *lepida* with ascending branches in small glandular inflorescence; 6*x*), 52% probability (Semple et al. 11157 WAT from Wildmint Hot Springs, Nahanni Nat. Park Reserve, Northwest Territories; var. *salerosa*; 2*x*), 50 % probability (*Chmielewski et al CC4714* WAT from N of Good Hope, British Columbia; var. *lepida* with very leafy inflorescence; 4*x*), and 50% probability (*Oldham & Sutherland 24798* WAT from Polar Bear Prov. Park, Ontario). Twenty-four specimens of the *S. lepida* a priori group plus one additional specimen added a posteriori were assigned a posteriori to the other groups: 13 specimens to *S. gigantea* with 88% probability (*Semple & Brouillet 7064* WAT from Boise Co., Idaho; var. *salebrosa* with sparsely pubescent mid and upper stem and glands in inflorescence; 6*x*), 83% probability (*Semple & Brouillet 7203* WAT; Teton Co., Wyoming; var. *salebrosa*; 6*x*), 74% probability (*Semple & Xiang 10329* WAT from Belt Mts., Broadwater Co., Montana; var. *lepida* with long ascending lower branches in leafy inflorescence; 6*x*), 68% probability (*Morton & Venn NA14185* TRT from Maidstone, Saskatchewan; var. *lepida* with glands on upper leaves, bracts and phyllaries), 67% probability (*Semple 10312* WAT from Powell Co., Montana; var. *lepida*; 6*x*), 61% probability (*Morton & Venn NA15876* TRT wild from Coconino Co., Arizona; var. *salebrosa*, a robust shoot with pubescent mid and upper stem and a narrow secund conical inflorescence; 6*x*), 60% probability (*Semple & Brouillet 4410* WAT from Lolo Pass, Idaho Co., Idaho; var. *salebrosa* with sparsely pubescent lower mid stem and densely so upper stem; 2*x*), 57% probability (*Morton & Venn NA14159* TRT from SE of Whitecourt, Alberta; var. *lepida* with leafy inflorescence with short ascending branches), 56% probability (*Semple & B. Semple 10622* WAT from NW of Jakey, Yukon Territory; var. *lepida*; 4*x*), 53% probability (*Morton & Venn NA13644* TRT from W of Vanderhoof, British Columbia; var. *lepida* with sparsely woolly stem and large inflorescence with long ascending branches; 6*x*), 43% probability (Rogers s.n. UBC from N of Trail, British Columbia; var. *salebrosa* with sparsely woolly proximally to densely woolly-strigose distally stem and a broadly spreading secund conical glandular inflorescence), 42% probability (*Morton & Venn NA14195* TRT from Battleford, Saskatchewan; *S. gigantea* like inflorescence but glandular; 6*x*), and 40% probability (*Semple & Brouillet 4381* WAT from Boundary Co., Idaho; var. *salebrosa*; lanceolate leaves with large serrations; 2*x*); and 11 specimens to *S. elongata* with 86% probability (*Eastham s.n.* UBC from between Kimberley and Fairmont, British Columbia; a small shoot with small heads; var. *salebrosa*), 82% probability (*Semple 11376 MONTU* from Lake Co. Montana; var. *salebrosa*; 2*x*), 79% probability (Melville BC6 WAT from Surrey, British Columbia; var. *lepida*; 6x), 78% probability

(*Semple & Xiang 10239* WAT from Carbon Co., Montana; var. *salebrosa*; 4x), 69% probability (*Chmielewski et al CC4760* WAT from Kitwanga, British Columbia; var. *lepida*), 69% probability (*Semple 11371* WAT from Lake Co., Montana; var. *salebrosa*; 2x), 65% probability (*Semple & Brouillet 4305* WAT from Nojack, Alberta; var. *lepida* with sparsely villous-strigose mid stem and leafy inflorescence with ascending branches), 62% probability (*Semple et al. 11169* WAT from Meilleur River Hotsprings, Nahanni Nat. Park Reserve, Northwest Territories; var. *lepida*; 2x), 56% probability (*Semple & Semple & B. Semple 5817* WAT from Boulder Co., Colorado; var. lepida with small glandular inflorescence; 6x), and 55% probability (*Morton & Venn NA14151* TRT from N of Wonowon, British Columbia; var. *lepida* with broadly lanceolate to narrowly ovate leaves and about average height involucres; 6x).

A two dimensional plot of CAN1 versus CAN2 canonical scores for 150 specimens of *Solidago elongata*, *S. gigantea*, and *S. lepida* is presented in Fig. 18. Eigenvalues on the first two axes were 1.092 and 0.445. Figure 19 is the same plot as Fig. 18 but with different symbols for the two varieties of *S. lepida.*

Two species level a priori groups analysis I

The Pearson correlation matrix of specimens of *Solidago elongata* and *S. lepida* yielded r > |0.7| for the following pairs of leaf traits reducing the number to be used: mid stem leaf length and upper stem leaf length, mid stem leaf length and upper stem leaf width, mid stem leaf width and upper stem leaf width, and ray floret ovary body length at anthesis and disc floret ovary body length at anthesis. Midstem stem leaf length and disc floret ovary body length at anthesis were included in the analysis.

In the STEPWISE discriminant analysis of 93 specimens of *Solidago elongata* and *S. lepida*, the following five traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: mid leaf length (22.37), disc lobe length (20.74), number of upper leaf margin serrations (11.81), disc corolla length (6.42), and number of ray florets (4.08). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. *Solidago elongata* and *S. lepida* had an F-to separate value of 16.977 (Wilks' lambda = 0.5062 df = 5 1 91; Approx. F= 16.9770 df = 5 87 prob. 0.0000).

In the Classificatory Discriminant Analysis of the two species level a priori groups, percents of correct a posterori assignment to the same a priori group were 96% for *Solidago elongata* and 82% for *S. lepida*. The Classification matrix and Jackknife classification matrix are presented in Table 7. Twenty-four of the 25 specimens of *S. elongata* were assigned a posteriori to *S. elongata*: 14 specimens with 93-99% probability, 4 specimens with 80-84% probability, 5 specimens with 70-77% probability (including *Semple & Brouillet 7114* WAT), and 1 specimen with 55% probability (*Semple & Brouillet 7132* WAT from Klamath Co., Oregon). One specimen of the *S. elongata* a priori group was assigned to *S. lepida* with 56% probability (*Wells 699* UBC from Tsawwassen, British Columbia; 110 cm tall shoot, mid to upper stem densely short hairy, inflorescence small but broadly secund conical; growing in very moist soil). Fifty-six of the 68 specimens of *S. lepida* were assigned a posteriori to the *S. lepida* group: 38 specimens with 92-100% probability, 12 specimens with 80-89% probability, 5 specimens with 70-79% probability, 2 specimens with 65% and 69% probabilities, and 3 specimens with 59% probability (*Morton & Venn NA15876* TRT cult. transplant from Coconino Co., Arizona; var. *salebrosa*; very robust lower and mid stem leaves; wild pressed shoot was assigned to *S. lepida* with 78% probability and was a robust shoot with a narrow secund conical inflorescence), 57% probability (*Semple et al. 9238* WAT from Summit Co., Utah; var. *salebrosa; 6x*), and 54% probability (*Morton & Venn NA14123* TRT from Liard Hot Springs, British Columbia; var. *lepida; 6x*).
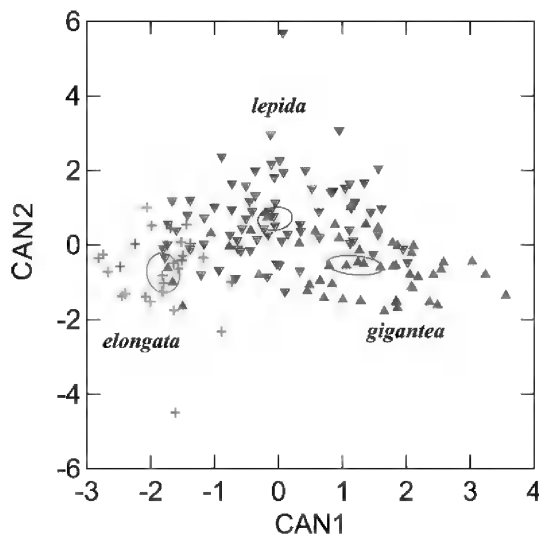
Figure 18. Two dimension plot of CAN1 versus CAN2 scores for 150 specimens of three priori groups of the *Solidago elongata* (orange +s), *S. gigantea* (blue triangles), and *S. lepida* (yellow inverted triangles); 95% confidence ellipses are shown for each taxon.
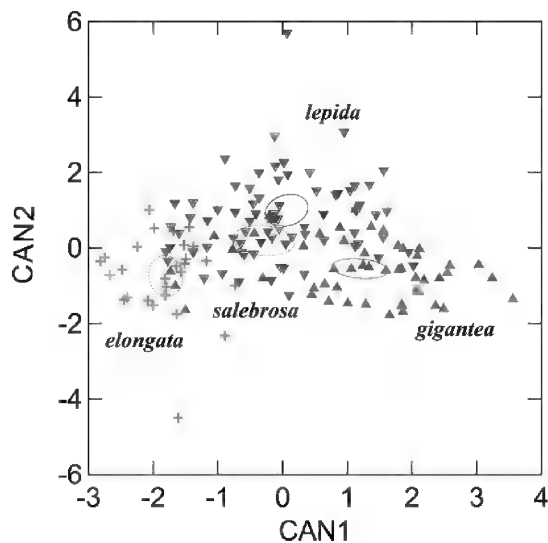

Figure 19. Two dimension plot of CAN1 versus CAN2 scores as in Fig. 17: *Solidago elongata* (orange +s), *S. gigantea* (blue triangles), and *S. lepida* var. *lepida* (yellow inverted triangles) and *S. lepida* var. *salebrosa* (red inverted triangles); 95% confidence ellipses are shown for each taxon.

Twelve specimens of the *S. lepida* a priori group were assigned a posteriori to *S. elongata* with the following probabilities: 91% probability (*Eastham s.n.* UBC from between Kimberley and Fairmont, British Columbia; a small shoot with small heads; var. *salebrosa*), 86% probability (*Semple 11376* WAT from Lake Co., Montana; small shoot, var. *salebrosa*; 2*x*), 85% probability (*Semple & B. Semple 11367* WAT from Custer Co., Idaho; var. *lepida*; 2*x*), 83% probability (*Semple 11376 MONTU* from Lake Co. Montana; var. *salebrosa*; 2*x*), 83% probability (Semple et al. 11169 WAT from Meilleur River Hotsprings, Nahanni Nat. Park Reserve, Northwest Territories; var. *lepida*; 2*x*), 77% probability (*Semple & Brouillet 4305* WAT from Nojack, Alberta; var. *lepida*; average height involucre), 76% probability (*Semple 11376 WAT* from Lake Co. Montana; var. *salebrosa*; 2*x*), 75% probability (*Semple & Xiang 10239* WAT from Carbon Co., Montana; var. *salebrosa*; 4*x*), 69% probability (*Morton & Venn NA14151* TRT from N of Wonowon, British Columbia; var. *lepida* with broadly lanceolate to narrowly ovate leaves; 6*x*), 68% probability (Melville BC6 WAT from Surrey, British Columbia; var. *lepida*; 6x), 60% probability (*Eastham s.n.* UBC from Waitabit Creek, British Columbia; a small shoot with small heads; var. *salebrosa*), and 44% probability (*Semple & Brouillet 4376* WAT from Moyie, British Columbia; var. *salebrosa*; 2*x*).

Frequencies of CAN1 canonical scores for 93 specimens of *Solidago elongata* and *S. lepida* are presented in histograms in Fig. 20. The Eigenvalue on the first axis was 0.976.

Table 7.   Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of two varietal level a priori groups; a posteriori placements to groups in rows.

Group	*elongata*	*lepida*	% **correct**
elongata	24	1	96
lepida	12	56	82
Totals	36	57	86

Jackknifed classification matrix

| Group	*elongata*	*lepida*	% **correct**
elongata	24	1	96
lepida	12	56	82
Totals	36	57	86
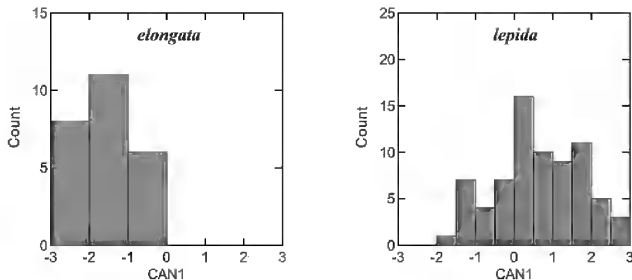
Figure 20.   Histograms of the frequencies of CAN1 scores for 93 specimens of *Solidago elongata* and *S. lepida*.

Two species level a priori groups analysis II

The Pearson correlation matrix for data on *Solidago gigantea* and *S. lepida* yielded r > |0.7| for the following three pairs of leaf traits reducing the number to be used: mid stem leaf length and upper stem leaf length, ray floret ovary body length at anthesis and disc floret ovary body length at anthesis, and ray floret pappus length and disc floret pappus length. Mid stem leaf length, disc floret ovary body length at anthesis, and disc floret pappus length were included in the discriminant analysis.

In the STEPWISE discriminant analysis of 116 specimens of *S. gigantea* and *S. lepida*, the following six traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: number of mid stem leaf margin serrations (19.52), ray floret lamina length (9.75), disc floret pappus length at anthesis (6.52), number of ray florets (5.96), involucre height (5.30), and number of upper stem leaf margin serrations (4.18). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. *Solidago gigantea* and *S. lepida* had an F-to separate value of 19.2000 (Wilks' lambda = 0.4862 df = 6 1 114; Approx. F= 19.2000   df = 6 109 prob. 0.0000).

In the Classificatory Discriminant Analysis of the two species level a priori groups, percents of correct a posterori assignment to the same a priori group were 87% for *S. lepida* and 81% for *S. gigantea*. The Classification matrix and Jackknife classification matrix are presented in Table 8. Fifty-nine of the 68 specimens of *S. lepida* plus 5 additional specimens included a posteriori were assigned a posteriori to *S. lepida*: 35 specimens with 90-100% probability, 6 specimens with 81-89% probability, 84 specimen with 70-78% probability, 5 specimens with 60-68% probability, and 2 specimens with 53% probability (*Morton & Venn NA14185* TRT from Maidstone, Saskatchewan; var. *lepida* with glands on upper leaves, bracts and phyllaries) and 51% probability (*Semple & Brouillet 4381* WAT from Boundary Co., Idaho; var. *salebrosa*; lanceolate leaves with large serrations; 2x). Nine specimens of the *S. lepida* a priori group were assigned to *S. gigantea*: with 86% probability (*Semple & Brouillet 4416* WAT from Missoula Co., Montana; var. *salebrosa* with lanceolate leaves with big serrations and small involucres), 84% probability (*Semple & B. Semple 5817* WAT from Boulder Co., Colorado; var. *lepida* with broadly lanceolate leaves and small club-shaped inflorescence with glands; 6x), 69% probability (*Semple & Brouillet 7203* WAT; Teton Co., Wyoming; var. *salebrosa*; 6x), 69% probability (*Semple & Heard 8130* WAT; Lincoln Co., New Mexico; var. *lepida* with ascending lower branches in inflorescence; 6x), 60% probability (*Semple & Brouillet 7066* WAT from Valley Co., Idaho; var. *lepida* with ascending branches in small glandular inflorescence; 6x), 60% probability (*Semple & Xiang 10329* WAT from Belt Mts., Broadwater Co., Montana; var. *lepida* with long ascending lower branches in leafy inflorescence; 6x), 57% probability (*Semple & Brouillet 7064* WAT from Boise Co., Idaho; var. *salebrosa* with sparsely pubescent mid and upper stem and glands in inflorescence; 6x), 52% probability (*Morton & Venn NA15876* TRT cult. transplant from Coconino Co., Arizona; var. *salebrosa*; very robust lower and mid stem leaves; 6x), and 52% probability (*Semple & Xiang 10243* WAT from Gallatin Co., Montana; var. *lepida* with large leaves in glandular inflorescence with ascending branches; 6x). Thirty-nine of the 48 specimens of *S. gigantea* were assigned a posteriori to the *S. gigantea* group: 24 specimens with 90-100% probability, 6 specimens with 83-88% probability, 4 specimen with 70-78% probability, 4 specimens with 63-69% probability, and 2 specimens with 54% probability (*Semple & Brouillet 6948* WAT from Douglas Co., Minnesota; glabrous upper stem, narrow upper stem lanceolate leaves with many large serrations and a damaged inflorescence with spreading arching branches; 6x) and 51% probability (*Cheek 1988* NH from KwalZulu-Natal, South Africa; this is a rather typical looks *S. gigantea* upper shoot).   Nine specimens of the *S. gigantea* a priori group with yellow rays were assigned a posteriori to *S. lepida*: with 95% probability (*Morton & Venn NA14213* TRT from Roblin, Manitoba; treated as *S. gigantea* but subsequently annotated as *S. lepida* aff. var. *lepida*; ascending

diverging lower inflorescence branches, glandular; 6*x*), 95% probability (*Morton NA18706* TRT from Crawford Co., Ohio; narrow lanceolate leaves with few small margin serrations, not glandular; 4*x*), 86% probability (*Semple 11523* WAT from York Co., New Brunswick; very sparsely glandular in narrow inflorescence), 78% probability (*Semple & Brouillet 7292* WAT from Bent Co., Colorado; leaves are lanceolate to narrowly lanceolate; 6*x*), 60% probability (*Cheek 1987* NH from KwalZulu-Natal South Africa; typical looking *S. gigantea*, not glandular), 59% probability (*Melville 984* WAT from Thunder Bay Dist., Ontario; leafy inflorescence with ascending-diverging branches; 4*x*), 58% probability (*Semple & B. Semple 11489* WAT from Cape Jourimain, New Brunswick; small leafy inflorescence with short diverging lower branches; 2*x*), 55% probability (*Melville 1666* WAT from Moosonee, Cochrand Dist., Ontario; open inflorescence with ascending lower branches; 4*x*), and 51% probability (*Semple & B. Semple 6718* WAT from Ingolf, Kenora Dist., Ontario; leaves are lanceolate; 6*x*).

Table 8. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of two varietal level a priori groups; a posteriori placements to groups in rows.

Group	*gigantea*	*lepida*	% correct
gigantea	39	9	81
lepida	9	59	87
Totals	48	68	84

Jackknifed classification matrix

Group	*gigantea*	*lepida*	% correct
gigantea	39	9	81
lepida	11	57	84
Totals	50	66	83

Frequencies of CAN1 canonical scores for 116 specimens of *S. gigantea* and *S. lepida* are presented in histograms in Fig. 21. The Eigenvalue on the first axis was 1.057.
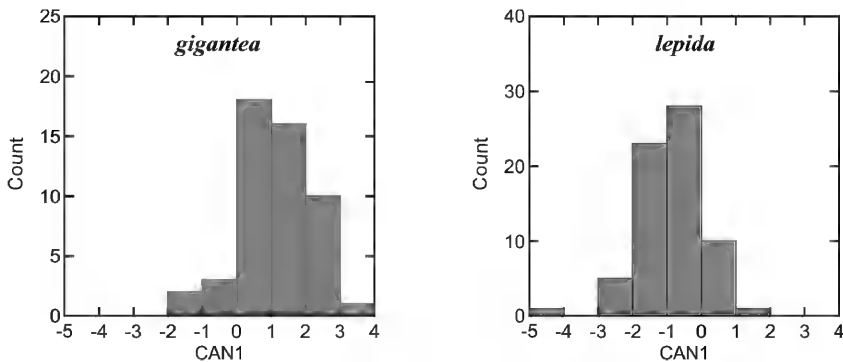
Figure 21. Histograms of the frequencies of CAN1 scores for 116 specimens of *Solidago gigantea* and *S. lepida*.

Two varietal level a priori groups analysis of *Solidago lepida*

The Pearson correlation matrix for data on *Solidago lepida* yielded r > |0.7| for the following four pairs of leaf traits reducing the number to be used: mid stem leaf length and upper stem leaf length, mid stem leaf width and upper stem leaf width, ray floret ovary body length at anthesis and disc floret ovary body length at anthesis, and ray floret pappus length and disc floret pappus length. Mid stem leaf length, mid stem leaf width, disc floret ovary body length at anthesis, and disc floret pappus length with included in the discriminant analysis.

In the STEPWISE discriminant analysis of 74 specimens of *Solidago lepida* var. *lepida* and *S. lepida* var. *salebrosa*, the following three traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: upper leaf width (24.85), number of mid stem leaf margin serrations (10.85), and disc floret ovary body length at anthesis (5.95). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The var. *lepida* and *var. salebrosa* had an F-to separate value of 12.994 (Wilks' lambda = 0.6423 df = 3 1 721; Approx. F= 12.9943 df = 3 70 prob. 0.0000).

In the Classificatory Discriminant Analysis of the two species level a priori groups, percents of correct a posterori assignment to the same a priori group were 90% for var. *salebrosa* and 73% for var. *lepida*. The Classification matrix and Jackknife classification matrix are presented in Table 9. Twenty-seven of the 30 specimens of var. *salebrosa* were assigned a posteriori to the var. *salebrosa* group: 5 specimens with 90-97% probability, 8 specimens with 80-89% probability, 8 specimens with 72-79% probability, 4 specimens with 61-67% probability, and 2 specimens with 55% probability (*Semple & Brouillet 7203* WAT; Teton Co., Wyoming; var. *salebrosa*; 6*x*) and 53% probability (*Semple 11376* WAT from Lake Co., Montana; small shoot with a narrow elongated inflorescence with ascending short branches longer than the subtending leaves; 2*x*). Three specimens of the var. *salebrosa* a priori group were assigned a posteriori to var. *lepida*: 1 specimen with 93% probability (*Morton & Venn NA14195* TRT from Battleford, Saskatchewan; var. *salebrosa* like inflorescence but glandular; 6*x*), 1 specimen with 90% probability (*Semple & Xiang 10324* WAT from Edith Lake, Belt Mts., Broadwater Co., Montana; leafy broadly secund conical inflorescence with ascending arching lower branches; 6*x*; Fig. 11), and 1 specimen with 73% probability (*Morton & Venn NA15876* TRT wild from Coconino Co., Arizona; var. *salebrosa*, a robust shoot with pubescent mid and upper stem and a narrow secund conical inflorescence; 6*x*). Thirty-two of the 44 specimens of var. *lepida* were assigned a posteriori to var. *lepida*: 10 specimens with 91-99% probability, 10 specimens with 80-89% probability, 5 specimens with 70-78% probability, 3 specimens with 62-67% probability, and 3 specimens with 56% probability (*Ringius et al. 940* WAT from Kapiskau R. near James Bay, Kenora Dist., Ontario; upper stem leaves are much reduced in the narrow inflorescence with ascending branches), 56% probability (*Chmielewski et al CC4714* WAT from N of Good Hope, British Columbia; very leafy inflorescence with ascending lower branches; 4*x*) and 51% probability (*Oldham 36842* WAT from Kenogami River junction with Little Drowning River, Thunder Bay Dist., Ontario; open leafy inflorescences with ascending arching lower branches). Twelve specimens of the var. *lepida* a priori group were assigned to var. *salebrosa* with 95% probability (*Chmielewski et al CC4231* WAT from Fairbanks, Alaska; leafy lower inflorescence, lower branches ascending or diverging; 2*x*), 83% probability (*Semple & Brouillet 7066* WAT from Valley Co., Idaho; ascending branches in small glandular inflorescence; 6*x*), 79% probability (*Semple & Heard 8130* WAT; Lincoln Co., New Mexico; ascending lower branches in inflorescence; 6*x*), 73% probability (*Semple et al. 11167* WAT, Virginia Falls float plane landing dock area, Nahanni Nat. Park. Reserve, Northwest Territories; small plant with small inflorescence with ascending lower branches 2*x*; Fig 7), 61% probability (*Chmielewski et al CC4285* WAT from Dalton Hwy at Yukon River, Alaska; small secund conical inflorescence and secund shoot with more club shaped inflorescence with ascending

branches; 2*x*), 61% probability (*Semple & B. Semple 11367* WAT from Custer Co., Idaho; leafy inflorescence with long ascending lower branches; 2*x*), 57% probability (*Oldham & Sutherland 25798* WAT from Polar Bear Prov. Park; small conical inflorescence with short spreading branches), 54% probability (*Morton & Venn NA14171* TRT from Elk Is. Nat. Park, Alberta; much reduce stem sparsely villous-strigose mid stem to more densely so distally, leaves just below small conical inflorescence; 6*x*), 54% probability (*Semple & Brouillet 4305* WAT from W of Nojack, Alberta; broad club shaped inflorescence with ascending to ascending arching branches), 52% probability (*Semple et al. 11167* WAT, Virginia Falls float plane landing dock area, Nahanni Nat. Park. Reserve, Northwest Territories; second shoot on sheet, small plant with small inflorescence with ascending lower branches 2*x*; Fig 7), 51% probability (55), and 51% probability (*Oldham & Sutherland 24804* WAT from Polar Bear Prov. Park, Ontario; leafy inflorescence with short ascending diverging lower branches).

Table 9. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of two varietal level a priori groups; a posteriori placements to groups in rows.

Group	lepida	salebrosa	% correct
lepida	32	12	73
salebrosa	3	27	90
Totals	35	39	80

Jackknifed classification matrix

Group	lepida	salebrosa	% correct
lepida	31	13	70
salebrosa	4	26	87
Totals	35	39	77

Frequencies of CAN1 canonical scores for 74 specimens of *S. lepida* var. *lepida* and var. *salebrosa* are presented in histograms in Fig. 22. The Eigenvalue on the first axis was 0.557.
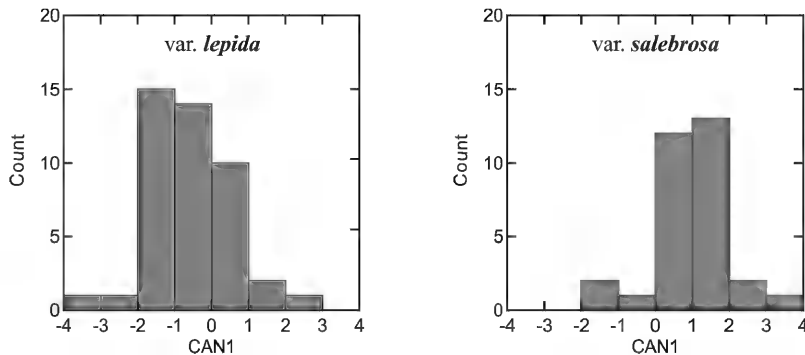
Figure 22. Histograms of the frequencies of CAN1 scores for 93 specimens of *Solidago lepida var. lepida* and var. *salebrosa*.

Two varietal level a priori groups analysis of *Solidago gigantea*

In the STEPWISE discriminant analysis of 49 specimens of *Solidago gigantea* var. *gigantea* and *S. gigantea* var. *shinnersii*, the following five traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: mid stem leaf width (11.42), upper leaf width (10.07), upper stem leaf length (9.21), outer phyllary length (4.29), and ray floret ovary length at anthesis (4.18). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The var. *gigantea* and *var. shinnersii* had an F-to separate value of 9.437 (Wilks' lambda = 0.4768 df = 5 1 47; Approx. F= 9.4365 df = 5 43 prob. 0.0000).

In the Classificatory Discriminant Analysis of the two varietal level a priori groups, percents of correct a posterori assignment to the same a priori group were 91% for var. *gigantea* and 87% for var. *shinnersii*. The Classification matrix and Jackknife classification matrix are presented in Table 10. Thirty-one of the 34 specimens of var. *gigantea* were assigned a posteriori to var. *gigantea*: 19 specimens with 93-100% probability, 4 specimens with 80-889% probability, 6 specimens with 70-77% probability, 1 specimen with 63% probability, and 4 specimens with 57% probability (Semple & Keir 4721 WAT from Cumberland Co., Nova Scotia; 2*x*), 55% probability (*Morton & Venn NA 17577* TRT from the Gaspé Peninsula, Québec; 4*x*), 55% probability (*Morton & Venn NA 17597* TRT from the Gaspé Peninsula, Québec; 4*x*) and 53% probability (*Semple & Brouillet 7373* WAT from Adams Co., Illinois; 4*x*). Four specimens of the var. *gigantea* a priori group were assigned to var. *shinnersii*: 91% probability (*Melville 1666* TRT, cult. transplant from Moosonee, Ontario; 4*x*), 84% probability (*Semple & Suripto 9871* WAT from Kakankee Co., Illinois; 4*x*), 71% probability (*Morton & Venn NA 17597* TRT from the Gaspé Peninsula, Québec; 4*x*), and 57% probability (*Melville 1685* WAT, from Timiskaming Dist., Ontario; 4*x*). Thirteen of the 15 specimens of var. *shinnersii* were assigned a posteriori to the var. *shinnersii* group: 8 specimens with 92-100% probability, 3 specimens with 80-89% probability, 1 specimen with 70% probability, and 1 specimen with 67% probability. Two specimens of the var. *shinnersii* a priori group were assigned a posteriori to var. *gigantea*: 1 specimen with 82% probability (*Semple & B. Semple 6718* WAT from Ingolf, Kenora Dist., Ontario; leaves are lanceolate; 6*x*) and 1 specimen with 78% probability (*Semple & Brouillet 7292* WAT from Bent Co., Colorado; leaves are lanceolate to narrowly lanceolate; 6*x*).

Frequencies of CAN1 canonical scores for 49 specimens of *S. gigantea* var. *gigantea* and var. *shinnersii* are presented in histograms in Fig. 23. The Eigenvalue on the first axis was 0.0.791.

Table 10. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of two varietal level a priori groups; a posteriori placements to groups in rows.

Group	*gigantea*	*shinnersii*	% correct
gigantea	31	3	91
shinnersii	2	13	87
Totals	33	16	90

Jackknifed classification matrix

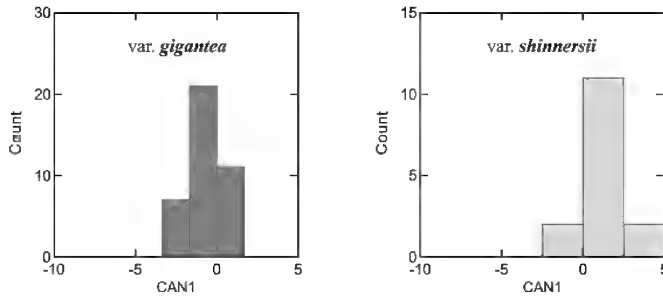| Group	*gigantea*	*shinnersii*	% correct
gigantea	30	4	88
shinnersii	2	13	87
Totals	32	17	88

Figure 23. Histograms of the frequencies of CAN1 scores for 93 specimens of *Solidago gigamtea var. gigantea* and var. *shinnersii.*

DISCUSSION

Five species level groups analysis

The results of the five species level analysis support the recognition of *Solidago altissima* (var. *gilvocanescens*), *S. canadensis*, *S. elongata* and *S. gigantea*, although only *S. canadensis* had strong statistical support (89% placement of specimens of the *S. canadensis* a priori group to the group a posteriori). Only 53% of the *S. lepida* a priori group specimens were placed into *S. lepida* a posteriori; 17.6% of the specimens were placed a posteriori into *S. altissima*, 17.6% of the specimens were placed a posteriori into *S. elongata*, 12.2% of the specimens were placed a posteriori into *S. gigantea*, and 0% were placed into *S. canadensis*.   However, no individuals of *S. lepida* had lower stem indument densities typical of *S. altissima* var. *gilvocanescens.*

No collections of *Solidago canadensis* from the Pacific Northwest were included in the analysis because none were seen in the 99 specimen UBC loan of "*S. canadensis*" nor in the numerous WAT and J.K. Morton TRT collections examined. A number of collections from British Columbia were included because they superficially looked like *S. canadensis* from eastern North America, but all were placed into western species a posteriori in the analyses. For example, *Eastham s.n.* (UBC) from Waitabit Creek west of Golden, British Columbia, was assigned a priori to *S. lepida* var. *salebrosa* and was placed in *S. lepida* with 50% probability (30% to *S. elongata*; 0% to *S. canadensis*) in the five species analysis, and with 61% probability (39% to *S. elongata*) in the three species analysis. UBC Specimens from British Columbia that had been annotated decades ago as *S. canadensis* were placed into *S. altissima* var. *gilvocanescens* or *S. lepida* var. *salabrosa* in the analyses were originally identified as these two taxa or *S. elongata*, but none as *S. canandensis*. The only UBC collection in the 99 specimens loan that was *S. canadensis* was from New Hampshire. *Solidago canadensis* is native to the northeastern USA and adjacent Canada and is not present in the Pacific Northwest (Semple & Cook 2006; Semple et al. 2013), except as possible garden cultivars.

Solidago altissima var. *gilvocanescens* is either native to a few valleys in southcentral and southeastern British Columbia or has been introduced from the prairies east of the Rocky Mts. and established. These plants can be a bit atypical for var. *gilvocanescens* but have the lower stem hair density of *S. altissima*. Two specimens from the Okanagan Valley in southeastern British Columbia that were assigned a priori to *S. altissima* were assigned a posteriori into *S. altissima* with 77% probability (*McCalla 8345* UBC) and 69% probability (*Gilmore 22* UBC); these both had moderately pubescent stems and leaf veins but otherwise fit well into *S. altissima*. *Canning s.n.* (UBC) from Penticton, British Columbia, was assigned a posteriori to *S. gigantea* with 72% (20% to *S. lepida* and

6% to *S. altissima*) but had the dense stem indument of *S. altissima* and not the glabrous to very sparsely hairy lower stems of *S. gigantea* and *S. lepida*. The plant was short but had robust serrate leaves on the lower and mid stem up to those subtending branches of the inflorescence and were reduced only in the inflorescence. The number of mid stem leaf margin serrations and mid stem leaf width were the second and third most important traits selected for discriminating a priori groups in the five species analysis. These traits were atypical for *Canning s.n.* (UBC) due to the short stature of the plant and few number of stem leaves.

Three species level groups analysis and the two species level groups analyses

The results of the analysis of specimens of *Solidago elongata*, *S. gigantea*, and *S. lepida* strongly support the recognition of *S. elongata* as a separate species, but indicate identification problems are likely with some western specimens of *S. gigantea* in areas where its range approaches or overlaps with *S. lepida*. All 28 specimens of *S. elongata* were placed a posteriori into *S. elongata* in the three species analysis and most were placed with high probability. One specimen, *Wells 699* (UBC) from Tsawwassen, British Columbia, was placed a posterori into *S. elongata* with 49% probability and slightly less so into *S. lepida*. The lower stem was sparsely canescent and the upper stem densely so; bracts in the inflorescence were obviously glandular. In the *S. elongata*/*S. lepida* analysis *Wells 699* (UBC) was placed a posteriori into *S. lepida* with 56% probability; all other specimens of *S. elongata* were assigned a posteriori to *S. elongata*. It is therefore possible that *Wells 699* (UBC) was assigned to the wrong species a priori. The presence of very glandular bracts is common in *S. lepida*, while the vegetation of *S. elongata* is glandless or has very few stipitate glands; if glands occur on the upper portions *S. elongata* they are very small and challenging to find. Based on observations from all other species of *Solidago*, a few glands might be encountered even on some individuals of species that usually have none.

In the three species analysis, 75% of *Solidago gigantea* specimens were assigned to *S. gigantea,* while 8 were assigned a posteriori to *S. lepida* and 4 to *S. elongata*. The ranges of *S. elongata* and *S. gigantea* are fully allopatric (Figs. 14 and 15) and mid stems of *S. elongata* are usually sparsely to moderately pubescent while those of *S. gigantea* are glabrous. In the two species analysis, 81% of the *S. gigantea* specimens and 87% of the *S. lepida* specimens were placed a posteriori into their respective a priori groups. Very small inflorescences of *S. elongata* (Fig. 2) and *S. gigantea* can be similar (which is true for most species of subsect. *Triplinerviae*), but mid to large ones are very different with those of *S. elongata* being non-secund and club shaped (Fig. 1) while those of *S. gigantea* are secund and conical (Figs. 4-6). Four of the *S. gigantea* specimens assigned to *S. lepida* were tetraploids from the eastern part of the range or invasive in the Old World. Six of the *S. gigantea* specimens assigned a priori to *S. lepida* were hexaploids from the western half of the range (Fig. 15) and only the specimen from Oklahoma was not from a part of the range that is, or potentially is, sympatric with the range of *S. lepida* (Fig. 16). The hexaploid *S. gigantea* specimen from Oklahoma was glandular in the inflorescence. The foothills of the Rocky Mts., the mixed prairie and mountain areas of Montana, along streams and rivers of the eastern Columbia R. drainage system, and the southern edge of the boreal forest-aspen parkland/prairie are the locations were the two species potentially come together and where hybridization between hexaploids is possible. It is not known whether hexaploid *S. gigantea* is natively more glandular in these habitats or whether the presence of such glands on inflorescence parts is evidence of hybridization with *S. lepida*. The Moss revised by Packer (1983) version of the Flora of Alberta did not deal with the problem and separated *S. gigantea* on stems being glabrous below the inflorescence and leaves being glabrous from *S. canadensis* (including *S. altissima* var. *gilvocanescens* as *S. canadensis* var. *gilvocanescens* and *S. lepida* as a synonym of var. *canadensis*) as having more hairy stems and leaves to varying degrees. Gland density was not discussed. The original version of the Flora of Alberta by Moss (1959) did treat *S. lepida* as a distinct species. Presence of stipitate glands in the infloresecence was not discussed.

The late J.K. Morton and the first author had multiple discussions over multiple years about the *Solidago gigantea/ S. lepida* problem, particularly along the northern edge of the prairie/forest ecotone. Most of the specimens from this area from central Alberta to southern Manitoba of uncertain placement in this study were glandular to some degree and were identified by J.K. Morton as *S. lepida*, while the first author's annotations often were *S. gigantea*. Although Cronquist (1994) may have felt that *S. lepida* belonged in *S. canadensis* as var. *salebrosa*, while *S. gigantea* was a readily recognizable species, the field and lab experiences of J.K. Morton and the first author of this publication disagreed with Cronquist. The real problem is convergence of hexaploid *S. gigantea* and hexaploid *S. lepida,* especially when the leaves of *S. gigantea* are not very broad for the western hexaploid cytotype, var. *shinnersii.* During early analyses of a smaller data set, all the glandular hexaploids from Alberta, Saskatechwan and Manitoba were treated as *S. lepida* and the results yielded much lower percents of correct a posteriori assignments to *S. gigantea* and *S. lepida.* When glands were ignored and only inflorescence branching pattern was emphasized, the a posteriori assignment results improved. Thirteen specimens, 8 of *S. gigantea* and 5 of *S. lepida,* in this study were collected in along a narrow strip from the western edge of Ontario across Manitoba and Saskatchewan to west-central Alberta; all whose chromosome numbers were determined were hexaploid while the ploidy level of the others was not determined. Opinions on the identity of a specimen and the multivariate results differed depending upon the specimen. The hexaploid *Morton & Venn NA14215* (TRT; Fig. 6) a cultivated voucher from a rootstock transplanted from southwestern Manitoba was assigned a posteriori to *S. gigantea* with 97% probability in both the three species and two species analyses involving *S. gigantea* and *S. lepida*; it was identified as *S. gigantea* by both J.K. Morton and by J.C. Semple. The hexaploid *Semple & Brouillet 4287* (WAT) from west of Elk Is. Nat. Park, Alberta was assigned a posteriori to *S. gigantea* in the five species analysis, the three species analysis, and the two species analysis with 80%, 90%, and 69% probabilities, respectively; it has glandular peduncle bracts and phyllaries; it was originally labeled *S. gigantea,* than annotated by J.C. Semple as *S.* aff. *lepida* in 2005 and then as *S. gigantea* in 2017. The hexaploid *Morton & Venn NA14195* (TRT; Fig. 23) from Battleford, Saskatchewan was identified as *S. lepida* by J.K. Morton and assigned a priori to *S. lepida* because it was obviously glandular in the inflorescence even though it had a relatively open secund conical inflorescence and had been annotated by J.C. Semple in 2017 it as *S. gigantea.* In the three species analysis, *Morton & Venn NA14195* (TRT) was assigned a posteriori to *S. gigantea* with 42% probability (41% to *S. lepida*), but in the two species analysis it was assigned to *S. lepida* with 67% probability. In the five species analysis, *Morton & Venn NA14195* (TRT) was placed a posteriori in *S. lepida* with 66% probability. Is it *S. gigantea* with glands or *S. lepida* var. *salebrosa* (and way east of the range of the variety) or *S. gigantea* × *S. lepida* var. *lepida*? Multivariate morphometric analysis does not provide a clear answer to this question. Which is more informative of identity, the number of mid stem leaf serrations included in the two species analysis or mid stem leaf length, disc corolla length and disc corolla lobe length included in the three species analysis? Both analyses included the number of upper stem leaf serrations, involucre height, number of ray florets, and ray floret lamina length. Using seven traits, *Morton & Venn NA14195* (TRT) was placed a posteriori in *S. gigantea* in the three species analysis, but using six traits it was placed a posteriori in *S. lepida* in the two species analysis. Technical traits requiring dissecting scope examination of parts were critical in both analyses. The final solution may come from DNA sequence analysis of multiple hexaploid plants of both species. *Morton & Venn NA14195* (TRT) will be annotated as *S. gigantea* × *S. lepida* var. *lepida* based on the ambiguous results. Two of the five specimens in the *S. lepida* a priori group from the Alberta to Ontario forest-prairie ecotone were assigned weakly to *S. gigantea* with 68% and 57% probability in the three species analysis but to *S. lepida* in the two species analysis with 53% and 70%, respectively. Based on inflorescence features these are all *S. lepida* var. *lepida.*
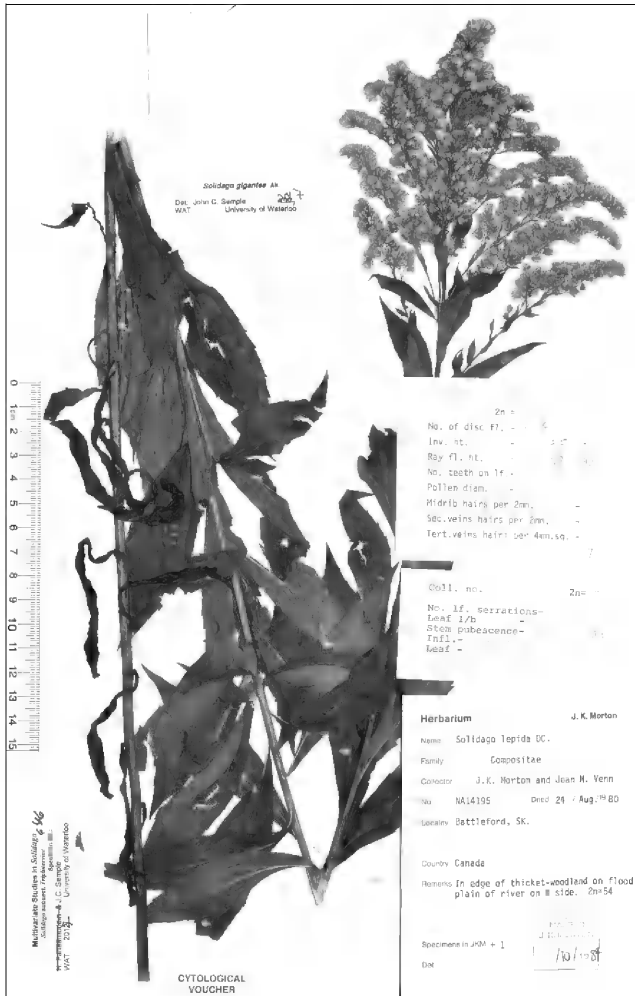
Figure 23. *Morton & Venn NA14195* (TRT) from Battleford, Saskatchewan. Is it *S. gigantea* with glands or *S. lepida* or *S. gigantea* × *S. lepida* var. *lepida*?

Included in the analyses were three hexaploid specimens treated a priori as *Solidago gigantea* from Idaho and eastern Washington. These represent a larger group of collections from southeastern British Columbia, eastern Washington and central and Northern Idaho area of very *S. gigantea*-like specimens, some of which are glandular and some of which are not. *Semple & Brouillet 4387* (WAT) from Whitman Co., Washington (very few glands on bracts and phyllaries), and *Semple & Brouillet 4403* (WAT) from Idaho Co., Idaho (glands on phyllary apices; Fig. 24), were assigned in the five

species analysis to *S. gigantea* with 97% and 100% probability, respectively; in the three species analysis *to S. gigantea* with 99% and 98% probability, respectively; and in the two species analysis to *S. gigantea* with 98% and 96% probability, respective. *Semple & Brouillet 4396* (WAT) from E of Lewiston, Idaho (glands on the upper leaves, peduncle bracts and phyllaries), was assigned a posteriori in the five species analysis to *S. lepida* with 74% probability, but to *S. gigantea* in the three species analysis and two species analyses with 98% and 83%, respectively. All three are mapped in the disjunct area of the range in Washington and Idaho on the range map of *S. gigantea* in Fig. 15. Potentially, *S. gigantea* occurs in scattered locations along streams and rivers further north and west in other areas of the Pacific Northwest including British Columbia, but the presence of some glands will make identification to *S. gigantea* rather than *S. lepida* more difficult. The occurrence of hexaploid hybrids between the two species in the Pacific Northwest is also possible, further complicating the identification task. No putative specimens of *S. gigantea* from British Columbia were included in the analyses. However, *F. Lomer 7497* (WAT, UBC) with immature heads from Castlegar, British Columbia, was annotated as *S. gigantea*; the ploidy level was not determined but the heads were small enough to possibly be diploid or tetraploid, which would make the collection introduced; if more mature heads would have been larger than it would likely be hexaploid and native. A collection from Okanagan, British Columbia (*Hill s.n.*, UBC), appears to be *S. gigantea*, but the collection consists of only one large stem leaf and a piece of stem with a small number of flowering heads.

Fig. 24. A shoot of *Solidago gigantea* from near Kooskia, Idaho held by graduate student at the time Luc Brouillet, 4 Sep 1979; the shoot grew along a river bank and was moved for the photograph.

The results of the multivariate analyses indicate that there is a problem with how best to treat the western diploids included in *S. lepida* in this study. Eight of the *Solidago lepida* specimens assigned a posteriori to *S. elongata* in the two species analysis were known diploids or likely diploids from southwestern Northwest Territories, eastern British Columbia, central Idaho, and western

Montana; most of these were small to mid height var. *salebrosa*. In contrast, 11 of the smaller var. *salebrosa* diploids from Alaska, Northwest Territories, Alberta, Idaho, Wyoming, and Colorado were placed a posteriori in *S. lepida* with high probabilies. Because diploids in *S. lepida* are generally less obviously glandular than polyploids, it is more difficult to identify the diploids as *S. lepida*. Many of these collections were originally identified as *S. elongata*, but all of them from were outside the range for the species shown in Fig. 14. When all the diploid *S. lepida* plants were placed into *S. elongata* or into their own a priori group in preliminary multivariate analyses, the results did not support these alternative interpretations as being more likely correct. Thus, all the diploids from the Rocky Mts. were included in *S. lepida* in the analyses presented here.

The following is a possible history of the *Solidago lepida* complex. It seems likely that at one point in the early history of *S. lepida* diploids were the only ploidy level in the species and these occurred in the Rocky Mts. from Alaska south to at least New Mexico and possibly south into eastern Mexico (no diploid counts are known for the species from Mexico). Tetraploids and hexaploids evolved from the diploids in the Rocky Mts., potentially multiple times, and these spread eastward all the way to northern Ontario and eastern Québec much more recently. Much earlier expansion(s) of the diploid range across Canada and subsequent isolation in glacial peak times is likely to have resulted in eastern diploids evolving in isolation into *S. brendiae*, *S. canadensis*, and *S. fallax*, although when is unknown. Diploids also expanded early into the Cascade Mts. in the Pacific Northwest, where they diverged and evolved in isolation into *S. elongata* with its distinctive inflorescence and very low numbers of or lack of glands and then spread south to the mountains in California. Some of the diploids of *S. lepida* in the Rocky Mts retained some of the more ancestral features and these are the specimens that were assigned a posteriori to *S. elongata* in the analyses, but are nonetheless individuals of *S. lepida*. When diploid *S. gigantea* diverged and evolved in eastern North America is also unknown. Whether it arrived along a southern route across North America or a more northern route from diploid southwestern ancestors is unknown, but we speculate here that an earlier divergence from diploid *S. lepida* or proto-*S. lepida* via a southern route into the southeastern USA is likely. From there the range expanded in part via the evolution of tetraploids and hexaploids into new habitats and subsequently westward across the Great Plains to the base of the Rocky Mts. from Alberta to New Mexico and further west in Montana into Idaho and Washington along rivers. British Columbia plants may be part of the western Columbia River drainage populations or more recent adventives from the western Canadian prairie populations.

Two variety level groups analysis of *Solidago lepida*

The results of the multivariate analysis of var. *lepida* and var. *salebrosa* provide support for recognizing the two varieties. In the two variety analysis, 90% of the var. *salebrosa* a priori group specimens were assigned a posteriori to var. *salebrosa*. One of the three specimens of var. *salebrosa* assigned a posteriori to var. *lepida* (*Semple & Xiang 10325*, WAT, a hexaploid from Montana; Fig. 12) clearly has the broad inflorescence with diverging lower branches characteristic of var. *salebrosa*, but was placed a posteriori into var. *lepida* with 90% probability. The mean value for upper stem leaf width was 8.25 mm for var. *salebrosa* and 12.5 mm for var. *lepida*. Thus, narrow upper stem leaves and arching spreading lower and mid inflorescence branches distinguish var. *salebrosa* from var. *lepida* most of the time. Some robust specimens of var. *salebrosa* have larger and broader upper stem leaves but still have the broad secund conical inflorescences with broadly spreading branches. In var. *lepida* the inflorescence branches are more often ascending, but in some cases branches are spreading but subtended by large leaves either much exceeding the branch length or nearly so. The ranges of the two varieties overlap throughout much of the western mountains. Further east var. *lepida* appears to be the only variety present, unless one includes some of those problematic *Solidago gigantea*-like plants in *S. lepida*. If so, then the range of var. *salebrosa* extends eastward to Saskatchewan in the forest-prairie ecotone. Our conclusion is that hybridization with *S. gigantea* may be occurring in the

ecotone area, yielding some odd *S. lepida* var. *lepida* plants or F1 hybrids with traits of both *S. gigantea* and *S. lepida*.

Two variety level groups analysis of *Solidago gigantea*

The results of the multivariate analysis of var. *gigantea* and var. *shinnersii* provides some support for recognizing the western hexaploids as the taxonomically distinct race var. *shinnersii*. The widths of mid and upper stem leaves are the most useful traits in separating the two varieties with means of 15.16 mm for mid stem leaves and 10.7 mm for mid and upper stem leaves var. *lepida* and 19.95 mm and 14.89 mm for var. *shinnersii*. All var. *shinnersii* plants with known chromosome number are hexaploid, but not all hexaploids have broad mid and upper stem leaves. This accounts for a posteriori correct assignment to a priori groups of 91% for var. *gigantea* and 87% var. *shinnersii*. Outer phyllary length and ray ovary body length at anthesis were also selected as useful in separating the two varieties and these traits are influenced by ploidy level and both were on average longer in var. *shinnersii* than var. *gigantea*. All three of the Washington and Idaho specimens of *Solidago gigantea* discussed above were placed a posteriori into var. *shinnersii* with 94-98% probability. One of the Alberta *S. gigantea* collections (*Turner* 3205, WAT) was treated as var. *gigantea* a priori and was placed into that variety a posteriori with 95% probability; the specimen included two smaller shoots with small narrowly lanceolate mid and upper stem leaves; the ploidy level is unknown. The other Alberta *S. gigantea* collection (*Semple & Brouillet 4287*, WAT) was a more robust hexaploid included in var. *shinnersii* a priori and was placed a posteriori in var. *shinnersii* with 89% probability. It is therefore possible, that growing conditions as indicated by plant height and leaf size may limit full development of the broad var. *shinnersii* form of mid and upper stem leaves. This would not be the case for environmentally stressed eastern plants because they would normally not produce very broad leaves under more favorable growing conditions. Three of the four var. *gigantea* specimens placed a posteriori into var. *shinnersii* were tetraploids from Illinois, northern Ontario near James Bay, and the Gaspé Peninsula, Québec. The fourth specimen was most likely tetraploid and was from Matachewan, Timaskaming Dist., in northern Ontario. Only the Illinois plant had leaves approaching the shape of those of typical var. *shinnersii*.

In conclusion, while there are difficulties in identifying individual specimens to species of subsect. *Triplinerviae* in the northern Cascade Mts., the mid latitude Rocky Mts., and the northern edge of the prairies into the adjacent woodlands across Alberta, Saskatchewan, and Manitoba, the following taxa should be recognized as native: *Solidago altissima* var. *gilvocanescens*, *S. elongata*, *S. gigantea* var. *shinnersii*, *S. lepida* var. *lepida*, and *S. lepida* var. *salebrosa*. *Solidago canadensis* is not native in western North America. The only modifications to the key to the subsection in Flora North America (Semple & Cook 2006) is the addition to *S. gigantea* of var. *shinnersii*, which is hexaploid, sometimes stipitate glandular on inflorescence parts, usually has broadly lanceolate to narrowly ovate midstem leaves, and has involucres at the higher end of the range for the species.

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NEW COMBINATIONS FOR SONORAN DESERT PLANTS

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ABSTRACT

We provide new nomenclatural combinations for three Sonoran Desert plants: **Opuntia engelmannii** var. **laevis** (J.M. Coulter) Felger, Verrier, & Carnahan, **comb. nov.**; **Parkinsonia florida** subsp. **peninsulare** (Rose) Hawkins & Felger, **comb. nov.**; and **Parkinsonia ×sonorae** (Rose & I.M. Johnston ex I.M. Johnston) Hawkins & Felger, **comb. nov.**

In the course of studies of Sonoran Desert flora (e.g., Felger et al. 2016, 2017a, 2017b) and sky islands in southern Arizona (Verrier in prep.), we find three taxa needing nomenclatural updates. The new combinations are provided below.

CACTACEAE

Opuntia engelmannii Salm-Dyck ex Engelm. var. **laevis** (J.M. Coulter) Felger, Verrier, & Carnahan, **comb. nov.** *Opuntia laevis* J.M. Coulter, Contr. U.S. Natl. Herb. 3: 419. 1896. *Opuntia phaeacantha* var. *laevis* (J.M. Coulter) L.D. Benson, Cacti Arizona (ed. 3), 21. 1969. **TYPE:** **Arizona**. [Pima Co.]: Santa Catalina Mountains, canyons, 17 May 1881, *C.G. Pringle s.n.* (holotype: F 92182).

Benson (1969) aligned this prickly pear with *Opuntia phaeacantha*. Pinkava (2003) relegated var. *laevis* to a synonym of *O. phaeacantha* but did not recognize varieties. However, plants from the type locality in the Santa Catalina Mountains are characteristic of *O. engelmannii*: the cladodes (pads) remain green all year, the flowers are relatively large, and the tepals are monochromatic yellow, becoming brownish-orange on the second day (Figures 1–3). In contrast, *O. phaeacantha* cladodes often become reddish-purple during winter and dry seasons, the flowers tend to be somewhat smaller, and the tepals are reddish basally, so that the flower is yellow with a reddish center. The fruits of var. *laevis* are relatively large, white-fleshed, and juicy, with a sweet flavor reminiscent of honeydew melon (other varieties of *O. engelmannii* are also fleshy but have reddish-purple fruit pulp and are also sweet but with a different flavor). The fruits of *O. phaeacantha* are smaller and the pulp is dull whitish, not very juicy, and not sweet. Like other forms of *O. engelmannii*, plants of var. *laevis* are relatively large and have an upright growth pattern, a stark difference from the low, sprawling form of

O. phaeacantha. Mature and older specimens of var. *laevis* become arborescent and can become massive, growing to 2.5 meters tall. Var. *laevis* occupies different habitats than those of *O. phaeacantha*, growing exclusively on cliffs, rock outcrops, and steep slopes. Var. *laevis* is a spineless or nearly spineless morphotype. Young plants are spiny for the first few years, and then begin to produce few-spined to essentially spineless cladodes.

<div align="center">FABACEAE</div>

Julie Hawkins and associates considered *Cercidium* to be a synonym of *Parkinsonia* based on phylogenetic studies which show *Cercidium* species nested with *Parkinsonia* (Hawkins 1996; Hawkins et al. 1999; Hughes et al. 2003). We provide new combinations for two taxa that have not been transferred from *Cercidium* to *Parkinsonia*.

Nine taxa of *Parkinsonia* trees are found in the Sonoran Desert. A key for the eight naturally occurring taxa is provided below. In addition, a horticultural selection of a hybrid found in the Tucson region –– *Parkinsonia* [*Cercidium*] cv. "Desert Museum" is grown in the Sonoran Desert region as a landscape tree. It involves hybridization of *P. aculeata*, *P. florida*, and *P. microphylla* (Dimmitt 1987). This hybrid is propagated by grafting onto *P. aculeata* rootstocks.

1. Leaves more than 10 cm long, pinnae usually strap-like (each pinna resembling an individual leaf) .... **Parkinsonia aculeata**
1. Leaves less than 7 cm long; pinnae usually not strap-like.

  2. Pinnae with (8) 16–45 pairs of leaflets .... **Parkinsonia ×carterae**
  2. Pinnae with 2–8 pairs of leaflets.

    3. Twigs spinescent at tip; axillary spines absent; petiole absent, the leaflets mostly 1–3.3 mm long .... **Parkinsonia microphylla**
    3. Twigs not spinescent at tip (sometimes moderately spinescent in *P.* ×*sonorae*); short axillary spines often present; leaves petioled, the leaflets mostly 2–10 mm long.

      4. Leaves with 1 pair of pinnae, each pinna with 2–4 pairs of leaflets .... **Parkinsonia florida**

      5. Branchlets glabrous or glabrate; leaflets 4–8 mm long, (2) 3 pairs per pinna; inflorescences relatively open; racemes including rachis mostly 1–4.5 (7) cm long; pedicels 6–12 (20) mm long; with age the upper petal usually orange-dotted .... **P. florida** subsp. **florida**
      5. Branchlets villous or pilose; leaflets 6–15 mm long, mostly 2 pairs per pinna; inflorescences relatively compact; racemes including rachis mostly 0.3–1 (2) cm long; pedicels 4–9 (12) mm long; upper petal not orange-dotted ...... **P. florida** subsp. **peninsulare**

      4. Leaves with 1 or 2 pairs of pinnae, each pinna with 4–8 pairs of leaflets.

      6. Spines 1 or 2 at each node, stout; petioles 4–21 mm long; leaflets 4–13 mm long; flowers including the banner bright yellow, the banner often with orange spots .... **Parkinsonia praecox**
      6. Spines 1 per node and slender, or absent; petioles to 3 mm long; leaflets 2–6 mm long; flowers pale yellow, the banner white to pale yellow without orange spots .... **Parkinsonia ×sonorae**

Parkinsonia florida (Benth. ex A. Gray) S. Wats. subsp. **peninsulare** (Rose) Hawkins & Felger,
    comb. nov. *Cercidium peninsulare* Rose, Contr. U.S. Natl. Herb. 8: 301. 1905. *Cercidium
    floridum* Benth. ex A. Gray subsp. *peninsulare* (Rose) A.M. Carter, Proc. Calif. Acad. Sci.,
    ser. 4, 40: 35. 1974. **TYPE: MEXICO**. [**Baja California Sur**]. Lower California, La Paz, 16
    Apr 1899, *E.A. Goldman 388* (holotype: US 360309, bar code 2535).

This subspecies is distinguished from subsp. *florida* by its generally larger leaflets, denser
and more persistent pubescence of larger hairs, differences in size of the inflorescences, and stoutness
of pedicels (Carter 1974; Hawkins 1996). Subsp. *peninsulare* occurs in Baja California Sur (Carter
1974), the south end of Isla Tiburón (Felger et al. 2001; Felger & Wilder 2012), and in Sonora in
Guaymas ("27°56'N, 110°49'W, 10 m elev, on the outskirts of the city," 27 Jan 1992, *Hughes 1562 et
al.*, MO) and on the coastal plain southward from Guaymas.

Parkinsonia ×sonorae Rose & I.M. Johnston ex I.M. Johnston) Hawkins & Felger, **comb. nov.**
    Cercidium sonorae Rose & I.M. Johnston ex I.M. Johnston, Contr. Gray Herb. 70: 66. [April]
    1924. **TYPE: MEXICO**. **Sonora**. Vicinity of Guaymas, dry hills, 10 Mar 1910, *Rose,
    Standley & Russell 12586* (holotype US 6354, bar code 2533).

Cercidium molle I.M. Johnston, Proc. Calif. Acad. Sci. 4, 12: 1038. [May] 1924. **TYPE: MEXICO**.
    [**Baja California Sur**]. In a wash at Agua Verde Bay, Lower California, 26 May 1921,
    Johnston 3877 (holotype CAS 1283; isotype UC 251946).

This natural hybrid between *Parkinsonia microphylla* and *P. praecox* occurs where the ranges of
the parent species overlap (Carter 1974). It is common in parts of western Sonora and relatively rare
in Baja California Sur (Carter 1974; Felger et al. 2001; Rebman et al. 2016; Turner et al. 1995).

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Figure 1. *Opuntia engelmannii* subsp. *laevis*. Grosvenor Hills on Salero Ranch, Santa Cruz Co., Arizona, 2 May 2011. Photo by Sue Carnahan.
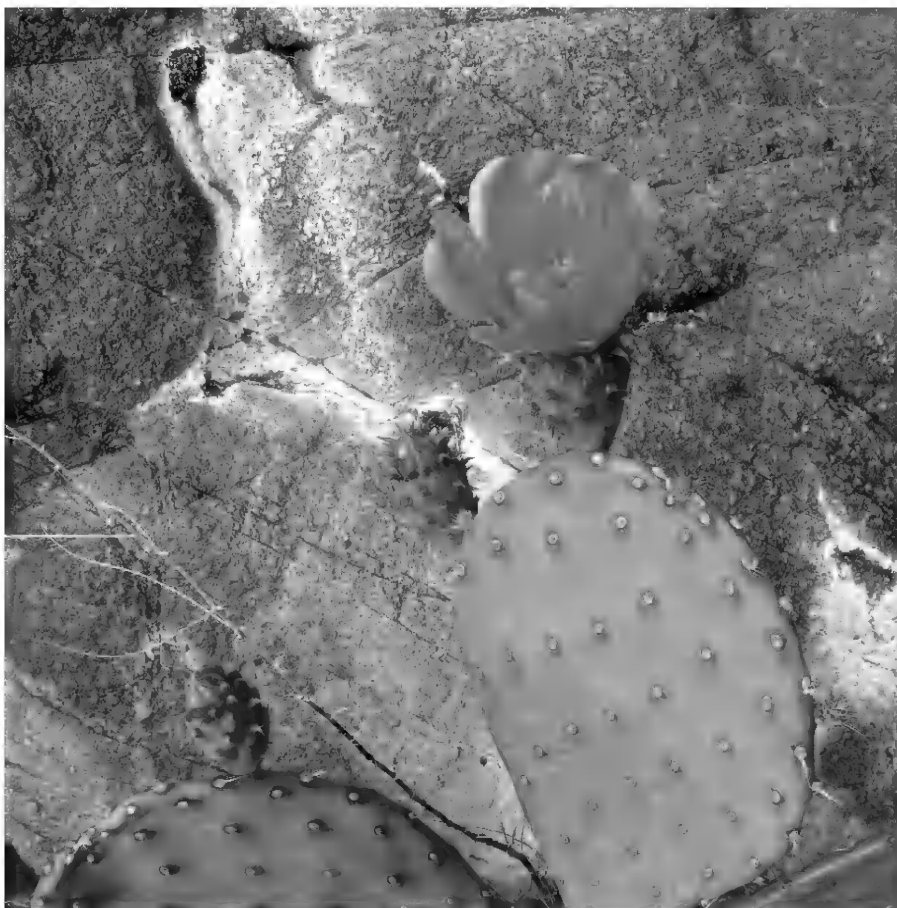
Figure 2. *Opuntia engelmannii* subsp. *laevis*. Grosvenor Hills on Salero Ranch, Santa Cruz Co., Arizona, 24 April 2011. Photo by Sue Carnahan.

Figure 3. *Opuntia engelmannii* subsp. *laevis*. An older flower, probably the second day; Diablo Canyon, Santa Catalina Mountains, Pima Co., Arizona, 11 May 2016. Photo by James Verrier.

UNA NUEVA ESPECIE DE *RHYNCHOSIA* (LEGUMINOSAE, PAPILIONOIDEAE) DE LA SIERRA MADRE ORIENTAL DE QUERÉTARO (MÉXICO)

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RESUMEN

Se describe e ilustra a ***Rhynchosia rosaurae*** Rzed., **sp. nov.**, del sector nororiental del estado de Querétaro, donde forma parte del bosque tropical caducifolio. La especie nueva pertenece a la sección *Copisma* y en sus características morfológicas parece relacionarse con *R. rojasii* Hassler, planta conocida de Argentina, Brasil, y Paraguay.

ABSTRACT

Rhynchosia rosaurae Rzed., **sp. nov.**, a component ot tropical deciduous forest of northeastern Querétaro, is described and illustrated. The new species belongs to the sect. *Copisma* and seems to be related to *R. rojasii* Hassler, a plant known from Argentina, Brazil, and Paraguay.

La preparación del segundo fascículo de Leguminosae, Papilionoideae para la Flora del Bajío y de regiones adyacentes reveló la presencia en Querétaro de una planta perteneciente a *Rhynchosia*, cuyas características morfológicas no corresponden a las de las especies conocidas de este género. En tal circunstancia se describe a continuación a:

RHYNCHOSIA ROSAURAE Rzed., **sp. nov.** **TIPO: MÉXICO. Querétaro.** Cerca de El Carrizal, municipio de Jalpan, fondo de cañada con vegetación de bosque tropical caducifolio, alt. 800 m, 12.XII.1988, trepadora herbácea, flores amarillentas, *J. Rzedowski 48103* (holotipo IEB; isotipos por distribuirse). Fig. 1.

Herba perennis volubilis; caules dense pilosi; folia trifoliolata, stipulae ovatae ca. 2 mm longae fere persistentes, stipellae absentes, petioli 2-6 cm longi, foliolorum laminae deltatae vel interdum ovatae, 2.5-8 cm longae et latae, apice acuminatae, base truncatae, utrinque piloso-sericeae, membranaceae; inflorescentiae laxe racemosae, ad 30 cm longae, (5)7-15-florae, bracteis lineari-lanceolatis 2-3 mm longis, pedicellis maturitate 5-7 mm longis; calyx 4-6 mm longus, dentibus triangularibus valde inaequalibus 0.5-3 mm longis, maturitate reflexis; corolla luteola 10-11 mm longa; stamina ca. 7.5 mm longa; fructus compressi oblongo-oblanceolati ca. 3 cm longi brunnei dense puberuli, ad basem saepe corrollae vestigiis instructi; semina ignota.

Planta herbácea perenne trepadora; tallos angulosos, densamente pilosos con pelos blanquecinos brillantes de ca. 1 mm de largo; estípulas ovadas, de ca. 2 mm de largo, densamente pilosas, al menos parcialmente persistentes, estipelas ausentes, peciolos de 2 a 6 cm de largo, con pubescencia similar a la de los tallos, foliolos 3, deltoides o a veces ovados, no pocas veces más anchos que largos, de 2.5 a 8 cm de largo y de ancho, acuminados a agudos en el ápice, truncados en la base, piloso-seríceos y suaves al tacto en ambas superficies, ciliados en el margen, con puntos glandulosos amarillentos en el envés, trinervados y con nerviación reticulada conspicua, de textura membranácea; inflorescencias en forma de racimos axilares largos, muy laxos, en fructificación hasta de 30 cm de largo, con (5)7 a 15 flores, pedúnculos hasta de 10(15) cm de largo, brácteas linear-lanceoladas, de 2 a 3 mm de largo, pronto caedizas, pedicelos en la madurez de 5 a 7 mm de largo; cáliz campanulado, de 4 a 6 mm de largo, densamente piloso por fuera, sus dientes triangulares,
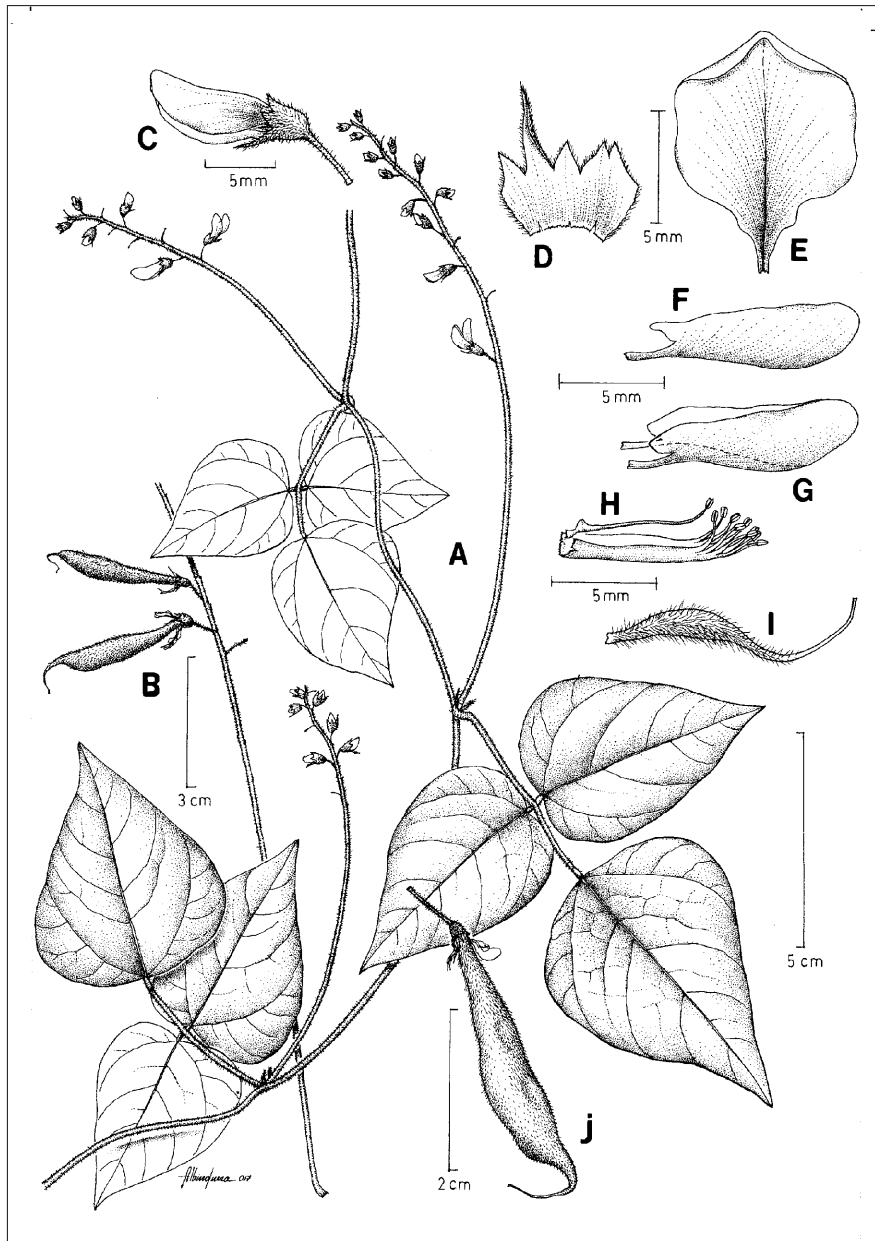
Figura 1. *Rhynchosia rosaurae* A. Rama con hojas e inflorescencias. B. Infrutescencia. C. Flor. D. Cáliz extendido. E. Estandarte. F. Ala. G. Quilla. H. Androceo. I. Gineceo. J. Fruto. Ilustrado por Albino Luna.

agudos en el ápice, el más largo de 2 a 3 mm de largo, a menudo más de dos veces más largo que los demás, reflejos en la fructificación; corola amarillenta, de 10 a 11 mm de largo, con frecuencia parcialmente persistente en la fructificación, estandarte de 10 a 12 mm de largo, con lámina casi orbicular, pubérula por fuera, su uña de 1 a 2 mm de largo, las aurículas diminutas, alas oblanceoladas, auriculadas en la base, de 9 a 10 mm de largo, glabras, sus uñas de ca. 2 mm de largo, los pétalos de la quilla oblanceolados, auriculados en la base, de ca. 8 mm de largo, glabros, sus uñas de ca. 2 mm de largo; androceo de ca. 7.5 mm de largo, anteras de poco menos de 1 mm de largo; ovario pubérulo, con el estilo manifiestamente encorvado; frutos oblongo-oblanceolados, fuertemente comprimidos, de ca. 3 cm de largo, de 4 a 5.5 mm de ancho, cafés oscuros, densamente pubérulos, el pico notablemente encorvado, de 2 a 5 mm de largo; semillas maduras desconocidas.

Rhynchosia rosaurae solo se conoce de la localidad tipo, ubicada en el sector nororiental del estado de Querétaro, perteneciente a la Sierra Madre Oriental. Es planta estrechamente endémica, escasa y vulnerable a la extinción, pues se registra de un área que ha sido intensamente explorada en tiempos relativamente recientes.

El nombre de la especie se dedica como homenaje a la Dra. Rosaura Grether González, destacada botánica mexicana, dedicada al conocimiento de la sistemática de la familia Leguminosae y colaboradora muy trascendente de la Flora del Bajío y de regiones adyacentes.

En virtud de sus frutos comprimidos y sin constricción, así como los lóbulos del cáliz del largo aproximado del tubo, la especie nueva se ubica en la sección *Copisma* (E. Mey.) Endl. (Grear 1978; Fortunato 2000). En sus inflorescencias largas y laxas, flores de ca. 10 mm de largo, estípulas más bien persistentes y frutos oblanceolados, *R. rosaurae* coincide y se relaciona al parecer con *R. rojasii* Hassler, planta conocida de Argentina, Brasil, y Paraguay. En el cuadro 1 se resumen las principales características diferenciales entre estos dos taxones.

	Rhynchosia rojasii	*Rhynchosia rosaurae*
Estipelas	presentes	ausentes
Foliolos		
forma	ovados a romboides	deltoides a ovados
base	obtusa a cuneada	truncada
Inflorescencias	con frecuencia ramificadas	sin ramificarse
Pedicelos, largo en la madurez	2 a 5 mm	5 a 7 mm
Androceo, largo	ca. 10 mm	ca. 7.5 mm
Fruto		
largo	4 a 4.5 cm	ca. 3 cm
ancho	7 a 9 mm	4 a 4.5 mm
pico	derecho	notablemente encorvado
Restos de la corola	ausentes en la base del fruto	a menudo presentes en la base del fruto

Cuadro 1. Principales características diferenciales entre *Rhynchosia rosaurae* y *R. rojasii*.

AGRADECIMIENTOS

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COMPOSITAE OF CENTRAL AMERICA–VIII.
THE GENUS *LEPIDAPLOA* (VERNONIEAE)

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ABSTRACT

The genus *Lepidaploa* (Compositae: Vernonieae), a segregate of *Vernonia*, is revised in Central America, where ten species are reported. New combinations are **Lepidaploa acilepis** (Benth.) Pruski, **comb. nov.**, **Lepidaploa argyropappa (**H. Buek) Pruski, **comb. nov**.*,* **Lepidaploa ovata** (Less.) Pruski, **comb. nov.**, and **Lepidaploa vernicosa** (Klatt) Pruski, **comb. nov.** The name of a widespread neotropical weed previously misidentified as *L. salzmannii* (a narrow Brazilian endemic) is here corrected to *L. argyropappa*. *Lepidaploa acilepis* is documented in Costa Rica and excluded from Mexico; *L. canescens* is recognized as distinct from *L. arborescens*; *L. chiriquiensis* is newly reported in Costa Rica; and *L. argyropappa* is newly reported in Panama. *Lepidaploa lehmannii*, formerly considered a South American endemic, is documented from Panama along the border with Colombia and is a new record for Central America. *Lepidaploa boquerona* is treated in synonymy of *L. tenella*, which is consequently a new record of the latter for Mexico. *Lepidaploa polypleura* is newly reported in El Salvador and Honduras, albeit from imperfect specimens. Lectotypes are designated for *Conyza uniflora* Mill. and *Vernonia lehmannii* Hieron. *Lepidaploa arborescens* is endemic to the West Indies, and both *L. remotiflora* and *L. salzmannii* are endemic to South America; each of the latter has been attributed previously to Central America but are here excluded.

The American genus *Lepidaploa* Cass. (Compositae: Vernonieae) is a segregate of *Vernonia* and contains about 150 Neotropical species. *Lepidaploa* as recognized currently is the largest genus of tribe Vernonieae, far outnumbering *Vernonia* sensu stricto in species. Similarly, Candolle (1836) recognized 290 species of *Vernonia*, with species numbers 64 (*V. zeylanica* (L.) Less.) to 259 (*V. tragiaefolia* DC.) treated in *Vernonia* sect. *Lepidaploa*, which as circumscribed by Candolle, however, contained both neotropical as well as paleotropical species.

Robinson (1990, 1999) resurrected *Lepidaploa* from synonymy with *Vernonia*, where most of its species were treated traditionally as *Vernonia* subgen. *Vernonia* sect. *Lepidaploa*, mostly there either without infrasectional placement or positioned variously in either subsect. *Graciles*, subsect. *Arborescentes*, subsect. *Scorpioides*, ser. *Canescentes*, ser. *Foliatae*, or the informal Lepidaploae Axiliflorae etc. (viz Candolle 1836; Bentham 1853; Baker 1873; Bentham & Hooker 1873; Hoffmann 1890–1894; Gleason 1906, 1922, 1923; Ekman 1914; Keeley & Jones 1977; Keeley 1978; Jones 1979). Regarding *Vernonia* sect. *Lepidaploa*, Gleason (1906) stated that "the close relationship of the *Scorpioideae foliatae* and *Scorpioideae aphyllae* is obvious" and that a "migration route through … Central America has been followed mostly by *Scorpioideae aphyllae*." It is perhaps noteworthy that in Central America 5 of our species are axillary-flowered and 5 are terminal-flowered and that Jones (1979) typified his *Vernonia* ser. *Canescentes* by *V. canescens* and his ser. *Foliatae* by *V. argyropappa*.

The segregate *Lepidaploa* most consistently differs from true *Vernonia* Schreb. (as well as from the large neotropical segregate *Vernonanthura* H. Rob.) by having echinolophate pollen (Robinson 1990, 1999, types C, D, and G; Keeley & Jones 1977, types B and C; Jones 1979, types B and C), generally sessile capitula (Figs. 1–2), and elongate-hexagonal (vs. quadrangular) pericarp raphide crystals (Fig. 3).

As mentioned above, *Lepidaploa* contains species often with capitula remote and sessile in the leaf axils forming interrupted leafy capitulescences (Figs. 1–2). These axillary-flowered species of *Lepidaploa* resemble many species of *Lessingianthus*, which differs by its sometimes quadrangular to elongate-hexagonal (vs. always elongate hexagonal) pericarp raphide crystals (Angulo et al. 2015) and simple (vs. nodular in *Lepidaploa*) style bases. A large number of *Lepidaploa* species, however, may have obviously terminal, aphyllous, seriated-cymose (not truly scorpioid) capitulescences (Figs. 9–10, 13; see Robinson 1990). The species of *Lepidaploa* with terminal capitulescences may resemble somewhat the genera *Cyrtocymura* H. Rob. and *Eirmocephala* H. Rob., each having only a single species in Central America. These two genera, however, differ from *Lepidaploa* by their densely truly scorpioid cymose capitulescence with curved apices and by pollen not always lophate.

Robinson (1999) treated *Cyrtocymura*, *Eirmocephala*, *Lepidaploa*, and *Lessingianthus* together in Vernonieae subtribe Vernoniinae. More recently, Keeley and Robinson (2009) described Lepidaploinae to include about a dozen genera (including the four genera aforementioned). In either subtribal system, *Lepidaploa* may be recognized by its capitulescence type and sessile capitula. The three other Central American genera of the Lepidaploinae (*Harleya* S.F. Blake, *Stenocephalum* Sch. Bip., and *Struchium* P. Browne; viz Pruski 2013), as well as the remaining South American genera do not seem overly similar to *Lepidaploa*. Although Central American *Lepidaploa acilepis* is so named for its resemblance in phyllary features to Asian *Acilepis* D. Don, which is not closely related and which differs from *Lepidaploa* by "unequal deeply separated cells" of the cypselar duplex trichomes and by usually "totally deciduous pappus" (Robinson & Skvarla 2009).

Figure 1. Field photograph of *Lepidaploa argyropappa* showing erect leafy flowering branches, sessile axillary capitula, outer phyllaries spreading and subulate-spinose, and the inner phyllaries more or less appressed and acuminate apically. The individual florets have lavender corollas and the pappus bristles are white. (*Pruski & Ortiz 4144*).

Figure 2. Field (roadside) photograph of *Lepidaploa tortuosa* showing an arching leafy flowering branch, sessile capitula, involucres of tightly appressed broad-tipped phyllaries, and white well-exserted corollas spreading laterally from the involucre. (*Pruski et al. 4239*).
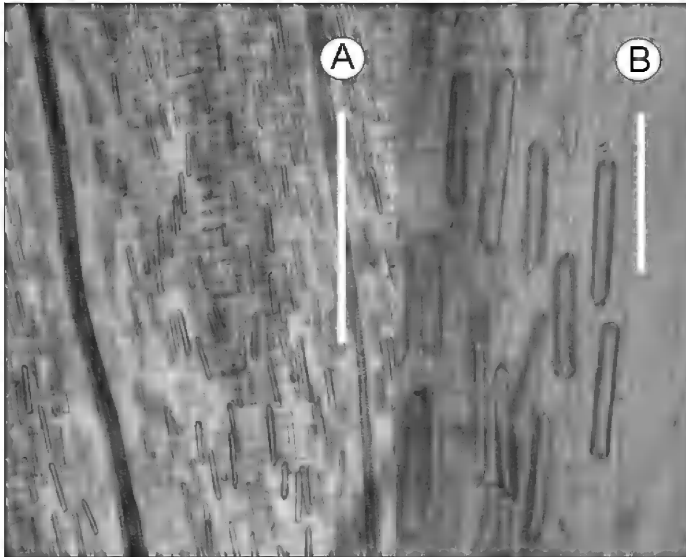
Figure 3. Elongate hexagonal pericarp raphide crystals in *Lepidaploa tortuosa*, typical of *Lepidaploa.* (Both from *Pruski et al. 4239*, MO; reprinted from Pruski 2016). [Scale bars: A 50 μm; B 10 μm].

In the discussion above and in what follows, species are generally referred to as *Lepidaploa* when nomenclatural combinations exist for them, even though called *Vernonia* in for example Gleason (1906, 1922, 1923), Keeley (2001), Nash (1976), and Turner (2007).

LEPIDAPLOA (Cass.) Cass., Dict. Sci. Nat. (ed. 2) 36: 20. 1825. *Vernonia* subgen. *Lepidaploa*
Cass., Bull. Sci. Soc. Philom. Paris 1817: 66. 1817. *Vernonia* sect. *Lepidaploa* (Cass.) DC.,
Prodr. 5: 26. 1836. LECTOTYPE (viz Robinson 1990): *Vernonia albicaulis* Vahl ex Pers. (=
Lepidaploa glabra (Willd.) H. Rob.).

   Annual or perennial herbs to subshrubs, vining shrubs, or trees to 7(–20) m; stems erect,
often branched, leafy, mostly pubescent, usually eglandular; herbage sessile-glandular or with simple
trichomes, trichomes never stellate or T-shaped.   **Leaves** alternate(-opposite), sessile or petiolate;
blade usually elliptic to ovate, mostly (stiffly) chartaceous, pinnately veined, never lobed, surfaces
usually concolorous. **Capitulescence** axillary of 1–few sessile capitula on leafy stems, or terminal
and held above leaves, seriated-cymose with repeated axillary-lateral branching overtopping-
displacing the more mature sessile (rarely pedunculate) previous capitulum, branch apices slightly
curved and somewhat arcuate, sometimes fractiflex, the maturation indeterminate (as is characteristic
of Compositae) but appearing determinate, capitula single or clustered, typically subtended by
reduced bracteate leaves, when obviously exserted and held above the axis unbranched for 5+ nodes,
the flowering branchlet main axis one per node. **Capitula** homogamous, discoid, mostly 8–60-
flowered, characteristically sessile or nearly so, very rarely obviously long-pedunculate (in
Mesoamerica only in *L. chiriquiensis*); involucre usually campanulate, terete in cross-section;
phyllaries usually more numerous than the florets, spirally imbricate, persistent but spreading laterally
post-fruit, graduate to merely slightly so with outer phyllaries sometimes more than half as long as the
inner, 3–6(–9+)-seriate, lanceolate (acicular to oblong), mostly green or purplish-tipped, margins
sometimes hyaline, often dimorphic, never long-appendiculate nor strongly colored throughout, the
outer phyllaries often spreading, commonly slender with aristate apices, the inner phyllaries
commonly erect with acute (acuminate-rounded) apices; clinanthium epaleate, commonly flat and
foveolate at anthesis, becoming convex and smooth post-fruit. **Florets** bisexual, 5-merous; corolla
actinomorphic or nearly so, never discoid-subligulate, pre-anthesis usually relatively narrowly
funnelform with a tube much longer than the limb to salverform with lobes spreading (coiling when
dried) near anthesis, throat usually much shorter than either the tube or the lobes (corolla infrequently
gradually and broadly funnelform short-tubed with and elongate throat), mostly violet throughout,
violet with a white tube, or white throughout, often papillose-setulose or glandular (but never
stipitate-glandular), especially so apically on the 5 elongate lobes, the tube generally glabrous, the
pair of marginal veins in the lobes usually relatively broadly fused apically; anthers with appendages
characteristically eglandular, infrequently glandular, spurred at base, the spurs polleniferous and
longer than collar; pollen echinolophate; styles branches ascending-elongate, filiform-subulate,
stigmatic surface continuous, shaft papillose distally, base with glabrous node. **Cypselae**
monomorphic, never carbonized, prismatic, commonly (5–)8–10-ribbed, generally setose with
antrorse duplex trichomes of equal appressed (infrequently divergent at apex) paired cells, often also
glandular, rarely solely glandular with no duplex trichomes, pericarp surface cells usually with
elongate hexagonal raphide crystals (Fig. 3; Robinson 1999; Pruski 2016); carpopodium well-
developed, symmetric, several cell layers tall; pappus double, never coroniform, white or dull white
to less commonly brown, persistent or inner bristles fragile with age, outer series of several distinct
short scales, inner series of many long straight bristles. n = 10, 16, 17 (but published miscounts
apparently frequent).

   Characters. The often used key character of the capitulescences being terminal and held
well above leaves vs. the capitulescences being leafy and axillary is a convenient and generally
trustworthy character.   The terminal vs. axillary character is usually diagnostic, but sometimes
aphyllous terminal flowered *L. canescens* may initiate flowering on extremely foreshortened axillary
branches (viz *Cándido 7*; and *King 5256* cited by Robinson 1990) and seems axillary-flowered.
Conversely, axillary-flowered *L. tortuosa* may have some leaves deciduous, thereby falsely appearing
terminal-flowered. Gleason (1906, 1922) treated usually terminal-flowered *L. canescens* in a group

apart from most species now referred to *Lepidaploa*. Similarly, Jones (1979) cited *Vernonia salzmannii* within ser. *Canescentes* and *V. argyropappa* as belonging to ser. *Foliatae*, but he subsequently (Jones 1980) treated them together as *V. salzmannii*, characterized by capitulescences "sparingly branched." Although inner phyllaries in *L. tortuosa* may vary from narrow to broad, they are always broad-tipped. The outer phyllary lengths relative to that of the inner phyllaries may vary in several species (e.g., *L. argyropappa*, *L. canescens*), but the outer phyllary shape is not very variable.

The corollas of *Lepidaploa acilepis*, *L. argyropappa*, and *L. uniflora* are distinctly tubular-funnelform, and those of *L. tortuosa* and *L. vernicosa* are relatively narrowly funnelform becoming slightly salverform. Those of *L. canescens* and *L. lehmannii* are short, obviously salverform, and basically without a throat. In each of the seven aforementioned species, the tube is as long as limb to much longer than limb. This is in contrast to the gradually broadly funnelform, moderately short-tubed *L. polypleura* and *L. tenella*. *Lepidaploa polypleura*, *L. tenella*, and *L. uniflora* are similar in having hairy corolla limbs, and in this regard stand apart from the other species. The most noteworthy species in corolla form is perhaps short-tubed gradually broad-funnelform or campanulate glabrous flowered *L. chiriquiensis*, which nevertheless has floral microfeatures (i.e., nodular style, and elongate-hexagonal pericarp raphide crystals) consistent with its placement in *Lepidaploa*. The corolla color of our species is mostly lavender to violet; *L. tortuosa* is odd in its white corollas. The five axillary-flowered species are those with the relatively long tubed-flowers, whereas the salverform and broad-flowered species are terminal-flowered.

Of our species, *Lepidaploa acilepis* and *L. uniflora* are the smallest herbs and *L. polypleura* is the tallest tree. *Lepidaploa uniflora* is totally different from all species by its glandular cypselae and adaxially obviously glandular leaves. *Lepidaploa tortuosa* and *L. vernicosa* are recognized by their unusually large capitula. Only *L. lehmannii* consistently displays glomerulate capitula. The most distinctive leaf venation and darkest pappus are those of plurinerved *L. polypleura*. *Lepidaploa argyropappa* and *L. canescens* are similar in their pilose leaves and commonly impressed-veined adaxial leaf surfaces, but mostly *L. argyropappa* is an axillary-flowered herb and *L. canescens* a terminal-flowered shrub. Further distinctions follow in the key below.

Distributions. The three most widespread species with nearly continuous distributions from Mexico to Panama are *Lepidaploa argyropappa*, *L. canescens*, and *L. tortuosa* (Pruski 2013). On rare occasions plants of *L. canescens* (especially in northern South America) have glabrous (not papillose-setulose or glandular) corolla tubes, and glandular-leaved *L. argyropappa* in the middle of Central America has longer outer phyllaries than does the type from Huánuco, but both are treated broadly here with no segregates used. However, *L. vernicosa* is pulled from synonymy of *L. tortuosa*, even though *L. tortuosa* occurs on all sides of the range of the narrowly endemic *L. vernicosa*.

I follow Ekman (1914), who noted that beginning with Baker (1873) the name *Lepidaploa salzmannii* has generally been misapplied (e.g., Jones 1980; Robinson 1990, 1999) to the widespread neotropical weed that occurs mostly from western Brazil and Peru northeastwards near continuously into Mexico. This weed is usually moderately pilose-leaved, nodally single-capitulate, and white-pappose: its name is changed here from *L. salzmannii* back to *L. argyropappa*. Moreover, Ekman (1914), in his summary of the *L. argyropappa* group, did not consider *L. salzmannii* as closely related to the *L. argyropappa* species group. Rather, *L. salzmannii* proves to have weakly pubescent leaves, mostly 2–3 small capitula per node, a tawny pappus, and is endemic to Brazil. The redefined *L. argyropappa* is among Brazilian species similar to *L. aurea* (Mart. ex DC.) H. Rob., which is a different, much more pubescent plant with adaxially glandular leaf blades.

Lepidaploa canescens is usually recognized by its small capitula, narrow inner phyllary apices, papillose-setulose or glandular corolla tubes, and terminal flowers. *Lepidaploa canescens* has a near continuous distribution from Central America into South America, so much so that although corolla tube papillosity varies in northern South America, segregates are hard to envision. West Indian *L. arborescens* (L.) H. Rob., however, appears geographically and morphologically distinct from it. On the other hand, a large geographic break occurs between morphologically similar sparsely pubescent *L. remotiflora* and more densely pubescent *L. acilepis*, and in this case the narrow species concepts used here are supported partly by allopatry. Other relatively narrowly endemics are *L. acilepis*, *L. chiriquiensis*, *L. polypleura*, *L. tenella*, *L. uniflora*, and *L. vernicosa*. *Lepidaploa lehmannii* is common in Colombia and Venezuela and newly reported here in Central America. In summary, Central American *Lepidaploa* more or less resembles most groups with about ten species, i.e., composed mostly of one to few widespread neotropical weeds (some of which are admittedly arbitrarily circumscribed and need further study), but the bulk of the group consists of narrowly defined regional endemics.

1. Capitulescence axillary and leafy; corolla tubes relatively long.

    2. Cypselae glandular; leaves obviously glandular adaxially .... **9. Lepidaploa uniflora**
    2. Cypselae rarely glandular; leaves not obviously glandular adaxially.

        3. Inner series of phyllaries constricted then distally dilated and cucullate, obtuse to rounded at apex .... **8. Lepidaploa tortuosa**
        3. Inner series of phyllaries never dilated, not cucullate, acute at apex.

            4. Capitula 12–18 mm long .... **10. Lepidaploa vernicosa**
            4. Capitula 7–12 mm long.

                5. Erect annual or short-lived perennial herbs 0.12–1 m tall; leaves widest at or above the middle of blade, eglandular abaxially .... **1. Lepidaploa acilepis**
                5. Perennial herbs or subshrubs 0.5–2 m tall; leaves widest in proximal 1/3 of blade, glandular abaxially .... **2. Lepidaploa argyropappa**

    2. Capitulescence terminal and held above stem leaves; corollas salverform or broad.

        6. Capitula often obviously pedunculate; corollas gradually broad-funnelform or campanulate .... **4. Lepidaploa chiriquiensis**
        6. Capitula sessile; corollas more or less broadly funnelform, but not campanulate.

            7. Shrubs to trees 3–19 m tall; stems angled; inner phyllaries broad-tipped .... **6. Lepidaploa polypleura**
            7. Subshrubs, shrubs, or vines 1–8 m tall; stems subterete; inner phyllaries narrow-tipped.

                8. Corolla tube papillose-setulose or glandular .... **3. Lepidaploa canescens**
                8. Corolla tube glabrous.

                    9. Terminal capitula glomerate .... **5. Lepidaploa lehmannii**
                    9. Terminal capitula usually 1–2 cm apart .... **7. Lepidaploa tenella**

1. LEPIDAPLOA ACILEPIS (Benth.) Pruski, **comb. nov.** *Vernonia acilepis* Benth., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1852: 68. 1853. **TYPE: NICARAGUA. Masaya**. Volcán Masaya, 2000 ft., Dec 1847, *Oersted 2/8528* (holotype: K-BENTH; isotypes: C, F, US). The holotype is numbered as *2* [perhaps a species number], but the isotypes are numbered "*8528.*" The isotype in C was photographed as Macbride number 22654, but was not seen on microfiche of the Copenhagen types (IDC microfiche 2204, card 214). Figs. 4, 5B.

Erect annual or short-lived perennial herbs 0.12–1 m tall; stems simple to few-branched, striate distally, thinly to moderately strigillose-villosulous, eglandular, somewhat sparsely leafy, internodes about 1/2+ as long as leaves. **Leaves** short-petiolate; blade 2.5–11 × 1–5 cm, elliptic to characteristically obovate (widest at or above the middle), thinly chartaceous, secondary veins 4–5 per side, often curving towards apex, both surfaces eglandular, adaxial surface smooth, thinly and sparsely to moderately villous-pilose adaxially and more densely so abaxially, trichomes 0.5–1+ mm long, basal cell of trichomes sometimes dark and leaves falsely appearing glandular, base cuneate to attenuate, margins subentire to serrulate, apex acute to acuminate; petiole 0.1–0.5 cm long. **Capitulescence** of axillary, remote, single(–3) capitula per node in smaller plants, in larger plants of (1–)3–5+ leafy seriated cymose branchlets in distal 1/2–2/3 of stem, each cymose branchlet 4–9+-capitulate, nodes usually 2–3 cm long, capitula single(–3) per node. **Capitula** 7–10 mm long, 12–19-flowered; involucre 7–9 × 4–8 mm long, turbinate-campanulate, nearly as long as florets; phyllaries 3–4-seriate, erect or outer ones somewhat spreading, villous-strigillose, eglandular; outer series of phyllaries 2–4 × 0.3–0.7 mm long, linear-lanceolate, about half as long as inner, 1-costate in distal 1/2, apex long-subulate with apical mucro 1–2 mm long; inner phyllaries 7–9 × 1.2–1.8 mm long, elliptic-lanceolate, margins scarious, purplish distally, apex acuminate. **Florets**: corolla 4–6 mm long, tubular-funnelform, pale pink to lavender, glabrous, tube often elongate, to ca. 4 mm long and obviously longer than the sometimes short limb, throat and lobes often nearly subequal, lobes ca. 1.1 mm long, eglandular. **Cypselae** 1.3–3 mm long, substrigose, trichomes to ca. 0.4 mm long, eglandular; pappus white or dull white or sometimes brown; outer squamellae 0.5–0.8 mm long; inner bristles 4–5 mm long, reaching to middle of corolla lobes.

Distribution and Ecology. *Lepidaploa acilepis* is an occasional regional Central American endemic known to me from only El Salvador, Nicaragua, and Costa Rica, where it is centered in the drier Pacific watershed. It was not reported in Honduras by Clewell (1975). The species should be looked for in Guatemala and Mexico, to where it has been attributed, but all collections from there examined by me are misdeterminations. *Lepidaploa acilepis* occurs from 100–700(–1500) meters elevation and has been collected in flower from September to December. Although long-known from Costa Rica based on B.L. Robinson's determination of *Tonduz 13595* (cited by Gleason 1906), *L. acilepis* was not treated by Standley (1938). The Gleason (1922) citation of the type locality as Costa Rican was erroneous, as Volcán Masaya instead is in Nicaragua. Vouchers cited by Gleason (1906) and those here, however, document the species in Costa Rica.

Representative collections. COSTA RICA. *Chavarria 887* (MO); *Chavarria 1324* (MO); *Chavarria 1968* (MO); *Grayum 12349* (MO); *Heithaus 482* (MO); *Opler 1579* (MO); *Tonduz 13595* (US). **EL SALVADOR.** *Calderón 1373* (US); *Castillo ISF00496* (B, K, LAGU, MO); *Rodríguez & Tejada 2152* (B, LAGU, MO); *Sandoval ES-01704* (B, EAP, K, LAGU, MO); *Tucker 440* (US). **NICARAGUA.** *Moreno 11715* (MO); *Neill 2856* (MO-2); *Neill 2925* (MO-3); *Stevens 10882* (MO).

Lepidaploa acilepis (as *Vernonia*) was recognized by Hemsley (1881), Gleason (1906, 1922), Nash (1976), Villaseñor (1989), and Keeley (2001) but reduced to synonymy with *L. remotiflora* (Rich.) H. Rob. by Robinson (1990), who was followed by Redonda-Martínez and Villaseñor (2011) and Pruski (2013). Here, Central American *L. acilepis* is resurrected from synonymy with South

American *L. remotiflora* as lectotypified by Pruski (1998). *Lepidaploa acilepis* differs from *L. remotiflora* by its corolla tube relatively longer, shorter eglandular corolla lobes, and more densely pubescent stems, adaxial leaf surfaces, and phyllaries. *Lepidaploa remotiflora* is thus excluded from Central America, with the collections from Costa Rica northwest into El Salvador proving instead to be *L. acilepis*. Material from Guatemala and Mexico previously identified as either *L. acilepis* or *L. remotiflora* are mostly redetermined as either *L. argyropappa* or *L. uniflora*.

Figure 4. Representative specimen of *Lepidaploa acilepis* showing leaves widest at or above the middle. (*Grayum 12349*, MO).
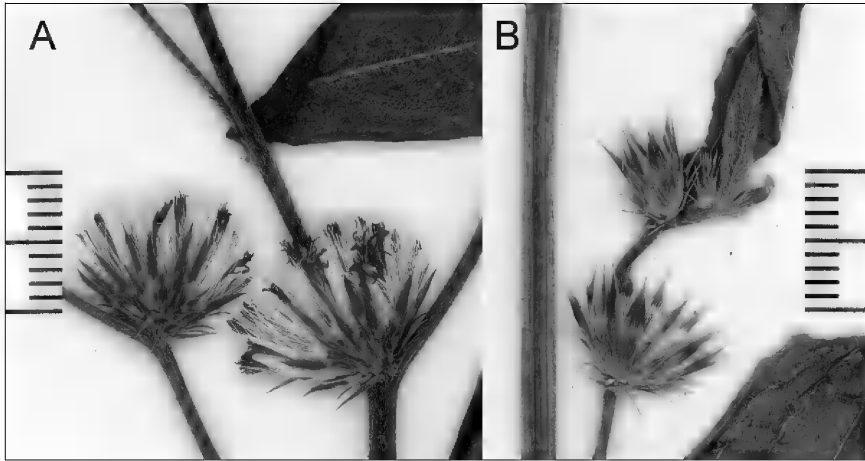
Figure 5. Involucres of (A) *Lepidaploa argyropappa*; and (B) *Lepidaploa acilepis*. In each species the outer phyllaries are acicular, and the apices of the inner phyllaries acute to acuminate. At anthesis the pappus bristles of *Lepidaploa argyropappa* (A) are about as long as the tubular-funnelform corollas. A metric scale is positioned vertically in each image. (A *Pruski & Ortiz 4144*, MO; B *Neill 2856*, MO, a topotype).

By its short stature and apically narrowed inner phyllaries, *Lepidaploa acilepis* among Central American Lepidaploas seems most similar to *L. uniflora* (Mill.) H. Rob. *Lepidaploa uniflora*, basically a Yucatán Peninsula endemic, differs from *L. acilepis*, however, by setose corollas limbs and by entire leaves glandular on both surfaces. By its small herbaceous habit and broad, thinly chartaceous leaves, *L. acilepis* is similar to Brazilian **Lepidaploa ovata** (Less.) Pruski, **comb. nov.** (basionym: *Vernonia ovata* Less., Linnaea 4: 294. 1829), which differs from *L. acilepis* by larger campanulate capitula, obtuse inner phyllaries, weakly pubescent leaves. Other similarly aristate-phyllaried regional species are *L. canescens* and *L. argyropappa*, but they are much taller plants.

Reports of the species in Guatemala and Mexico were not verified by me. Collections determined earlier as either *Lepidaploa acilepis* or *L. remotiflora* but here redetermined as other species include: (1) *Cowan 2773* from Tabasco cited by Cowan (1983) as *L. acilepis* is a misdetermination of the similar *L. argyropappa*; (2) *Croat 47502* from Chiapas cited by Redonda-Martínez and Villaseñor (2011) as *L. remotiflora* proves instead to be *L. tortuosa*; (3) *Orellana 50* from Guatemala distributed from BIGU as *L. acilepis* is determined here as *L. argyropappa*; (4) *Contreras 9347* (US) from Guatemala annotated *in sched.* in 1983 by Keeley as *V. acilepis* is *L. argyropappa*. Standley and Steyermark (1940: 394) reported *Standley 59631* (F) from Fiscal as *L. acilepis*, and commented that only a single plant was found. Guatemalan collections also determined *in sched.* by Jones and Keeley as *V. acilepis* include *Steyermark 31195* (NY) and *Standley 59192* (NY). Nash (1976: 21) also reported *L. acilepis* in both Guatemala and Chiapas, but I do not have at hand the collections seen by her. Her report of *L. acilepis* in Jutiapa is not based on the above Standley or Steyermark material. Although I do not have at hand *Standley 59192*, *Standley 59631*, *Steyermark 31195*, and all Chiapas collections, *L. acilepis* should nevertheless be looked for in Guatemala, especially given that Samuel Jones, Sterling Keeley, Rosario Redonda-Martínez, Dorothy Nash, Paul Standley, Julian Steyermark, and José Luis Villaseñor are renowned specialists and their determinations can be trusted. On the other hand, I cannot verify that *L. acilepis* occurs in Chiapas, and the species is excluded provisionally from Mexico.

2. LEPIDAPLOA ARGYROPAPPA (H. Buek) Pruski, **comb. nov.** *Vernonia argyropappa* H. Buek, Gen. Sp. Synon. Cand. 2: v. 1840. [this is a nom. nov. in the preface and numbered using the Roman numeral v; the page numbered page 5 using Arabic numerals is a different page having some of the index to genera that begin with the letter A]. *Vernonia poeppigiana* DC., Prodr. 5: 55. 1836 (non DC. 5: 20. 1836). *Vernonia geminiflora* Poepp., Nov. Gen. Sp. Pl. 3: 42. 1843, nom. superfl. **TYPE: PERU. Huánuco.** Prope Cuchero, Jul 1829, *Poeppig* pl. exs. n. *1204* [species number 31] (holotype: G-DC, as Macbride neg. 8135, as IDC microfiche 800. 774.III.8; isotypes: F, HAL, NY, W). Pruski (2012) gave the Ruiz and Pavón and Poeppig locality of Cuchero (abandoned when visited by Poeppig) as "near modern day San Juan, and about 4–8 km SW of the boca del Río Chinchao at the Río Huallaga, 9° 30–31' S, 75° 56–59' W." Poeppig (1843) gives the locality more precisely as at Pompayaco [aka Pompayacu], which is at 9° 33' 28" S, 75° 54' 35" W or about 6 km SE of Cuchero and just across (east of) río Huallaga. Figs. 1, 5A, 6–8.

Cacalia argyropappa (H. Buek) Kuntze*, Cacalia virens* (Sch. Bip. ex Baker) Kuntze, *Vernonia friedrichsthalii* Sch. Bip. ex Ekman, *Vernonia guianensis* V.M. Badillo, *Vernonia miersiana* Gardner, *Vernonia virens* Sch. Bip. ex Baker

Perennial herbs (less commonly perhaps subshrubs) 0.5–2 m tall; stems erect, simple or few-branched, striate, hirsute to pilose with appressed or ascending trichomes. **Leaves** subsessile or short-petiolate; blade 3–14(–18) × 0.7–3.5(–8) cm, lanceolate to elliptic-lanceolate or rarely oblanceolate, usually widest in proximal 1/3 of blade, chartaceous, secondary veins usually 4–6 per side, sometimes obviously impressed adaxially, prominent abaxially, strongly arching toward apex, surfaces concolorous to sometimes somewhat discolorous, adaxial surface puberulent to hispid or strigose, eglandular, veins often impressed with surface appearing rugulose, abaxial surface strigose to pilose-villous with trichomes to ca. 1+ mm long, typically patent-antrorse, also glandular, base cuneate or obtuse to sometimes rounded, margins usually entire or sometimes minutely serrulate, sometimes subrevolute, apex acute to acuminate; petiole 0.1–0.5 cm long. **Capitulescence** of leafy few-branched weak seriate-cymes, ultimate branches usually 10–15 cm long, 5–12-capitulate, capitula sessile, remotely spaced (internodes 1–3 cm long) and capitula at anthesis always subtended by a leaf much larger than capitulum, capitulescence leaves similar to vegetative leaves but slightly smaller. **Capitula** 9–12 mm long, 21–35(–40)-flowered; involucre 6–10 × 9–14 mm, campanulate to nearly hemispheric, phyllaries moderately graduate with outer usually at least about half as long as inner, 4–6-seriate, outer and mid-series phyllaries pilose to inner series only sparsely pilose; outer and mid-series phyllaries 3–6 × 0.3–0.8 mm, linear-lanceolate, sometimes recurved, outer series with somewhat thickened pale midrib extending into subulate-subspinose apex, mid-series narrowly attenuate, not spinulose, without midrib prominulous distally; inner series of phyllaries 6–10 × 1–1.5 mm, lanceolate, the thin midrib pale sometimes purplish, apex acuminate; clinanthium to 3 mm diam., often dome-shaped. **Florets**: corolla 5–8 mm long, sometimes those of the marginal florets noticeably longer than those of the central florets, tubular-funnelform, reddish-purple, glabrous, or apex of lobes sometimes papillose-glandular, tube elongate, 3.5–4.5 mm long, gradually widening into throat, often noticeably longer than limb, lobes 1–1.6 mm long. **Cypselae** 1.5–2.8 mm long, densely substrigose to hirsutulous, usually eglandular or sometimes at maturity glandular especially proximally (sometimes with resiniferous idioblasts prominent throughout); pappus white or dull white, outer squamellae 1–1.5 mm long, inner bristles 6–8 mm long, usually slightly exserted from involucre.

Figure 6. *Lepidaploa argyropappa* line drawing showing impressed secondary veins. Reproduced from Pruski 1997, Fig. 256.

Distribution and Ecology. *Lepidaploa argyropappa* is widespread in the Neotropics, occurring in Mexico, Central America, Colombia, Venezuela, Guyana, Ecuador, Peru, Bolivia, and western Brazil. In Central America it occurs from near sea level to 1800 meters elevation, flowers mostly from December to May, and seems only to have not been collected in flower in July. It is noteworthy, however, that this widespread moderately common species was not cited by Elias (1975), Correa et al. (2004), or Pruski (2013) for Panama, where it represents a new record.

Representative collections. **BELIZE.** *Bartlett 11340* (MO, US); *Davidse & Brant 32472* (MO, US); *Gentle 3889* (MO, NY); *Gentle 8144* (MO, NY, TEX); *Schipp 85* (MO, NY). **COSTA RICA**. *Haber & Zuchowski 10478* (CR, MO, TEX); *Pittier 3252* (US; cited by Klatt 1892 as *Vernonia remotiflora* var. *tricholepis*; *Pittier 12159* (US); *Skutch 2385* (MO, US); *Skutch 4176* (MO, US); *Tonduz 13268* (US); *Wilbur & Stone 10098* (MO, US). **EL SALVADOR.** *Standley 21565* (US); *Tucker 771* (US). **GUATEMALA**. *Contreras 9347* (MO, US; cited in Villaseñor 1989: 108 sub *Vernonia argyropappa*; US annotated by Keeley 1983 as *V. acilepis*); *Orellana 50* (BIGU, MO; distributed to MO as *V. acilepis*); *Véliz 95.4360* (BIGU, MO); *Williams et al. 42204* (F, NY, US). **HONDURAS**. *Blackmore & Heath 1602* (BM, MO); *Croat & Hannon 64442* (MO, US); *Nelson et al. 7905* (MO, UC, US). **MEXICO. Chiapas**. *Matuda 1914* (MEXU, MO, TEX, US); *Méndez Ton (Shilom Ton) 5733* (IEB MEXU, MO). **Tabasco.** *Cowan 2773* (CAS, ENCB, MEXU, MO, NY). **Veracruz.** *Pruski & Ortiz 4144* (MO, XAL). **NICARAGUA**. *Atwood 4018* (BM, F, GH, MO); *Proctor 27397* (NY, US); *Rueda 15806* (MO, US); *Stevens 7367* (MO). **PANAMA**. *Correa et al. 4786* (MO, PMA); *Correa et al. 10492* (PMA, US); *Galdames & Stapf 5391* (US).

Figure 7. Isotype of *Vernonia poeppigiana* [≡ *Lepidaploa argyropappa*] showing the somewhat discolorous leaves and axillary capitula. (*Poeppig* pl. exs. n. *1204*, NY).

Figure 8. Representative specimen of *Lepidaploa argyropappa* showing the relatively large, axillary capitula. (*Pruski & Ortiz 4144*, MO).

In Central America, the name *Lepidaploa argyropappa* has usually been used for our plants (e.g., Gleason 1906, 1922; Standley 1938; Clewell 1975; Nash 1976; Jones 1979; Villaseñor 1989; Rzedowski & Calderón de Rzedowski 1995; Keeley 2001). Ekman (1914) in his key to "The allies of *Vernonia argyropappa* H. Buek," recognized *V. argyropappa*, *V. hirsutivena* from the Yucatán (= *L. canescens*), and *V. miersiana* Gardner [which included fide Ekman 1914 *V. salzmannii* DC. sensu Baker (1873) non DC. 1836]. Ekman (1914) segregated from *L. argyropappa* more strongly cuspidate-phyllaried *V. friedrichsthalii* Sch. Bip. ex Ekman, which is based presumably on material from either Nicaragua or Costa Rica. Nash (1976) gave *V. friedrichsthalii* as a nomen and in synonymy with *L. argyropappa*. *Vernonia miersiana* Gardner was treated in synonymy with *L. salzmannii* by Robinson (1990, 1999), but I do not have material of it at hand and leave it unplaced. Material from Costa Rica and Nicaragua often has longer outer series of phyllaries than, for example, Andean and Mexican plants, but across the species range there seems to be a continuum in outer phyllary lengths relative to that of involucres and segregates are not recognized here.

After Jones (1980) in Flora of Peru treated *Lepidaploa argyropappa* in synonymy with *L. salzmannii* and Robinson (1990, 1999) resurrected *Lepidaploa*, however, the name *L. salzmannii* has been adopted uncritically (e.g., Pruski 1997, 2013; Turner 2007; Nelson 2008; Redonda-Martínez & Villaseñor 2011). Here, too, the common Neotropical species is interpreted broadly but excludes the type of *V. salzmannii* from Bahia, which is a very different plant that is weakly pubescent leaved, mostly 2–3 nodally capitulate, and has a tawny pappus. The name *Vernonia velutina* Hieron. from Rio de Janeiro has occasionally been treated in synonymy of *L. salzmannii* sensu auct., but by its terminal capitulescence is excluded here from synonymy of each *L. argyropappa* and *L. salzmannii*.

By similar glandular leaves axillary-flowered *Lepidaploa argyropappa* recalls *L. canescens*, which differs usually by its terminal flowers and papillose-setulose corolla tubes. By relatively large capitula *L. argyropappa* is somewhat similar to *L tortuosa*, but *L. argyropappa* differs by basically subsessile chartaceous leaves, by corolla lobes only 1–1.6 mm long, by outer and mid-series phyllaries often more pubescent than inner phyllaries, and by subequal outer and mid-series phyllaries with midrib indistinct or merely prominulous. The corolla tube *of L. argyropappa* often noticeably elongates during flower. The citation by Sousa and Cabrera (1983) and Martínez et al. (2001) of *L. argyropappa* in Quintana Roo and Campeche, respectively, are based on misdeterminations of vouchers referred here to *L. uniflora*.

3. **LEPIDAPLOA CANESCENS** (Kunth) H. Rob., Proc. Biol. Soc. Wash. 103: 483. 1990. *Vernonia canescens* Kunth, Nov. Gen. Sp. (folio ed.) 4: 27, tab. 317. 1820 [1818]. **TYPE: PERU. Piura.** Prope Huancabamba (as "Guancabamba"), 127 hex, (?Apr–?Aug) 1802, *Humboldt & Bonpland 3529* (holotype: P-HBK, as IDC microfiche 6209 91.II.5; isotype: P, as Macbride neg. 37320). Sandwith (1968) gave as Aug 1802 the date of the Huancabamba collections, but the protologue noted the flowering epoch as April, conflicting with Sandwith. Humboldt material in B-W and HAL may be type material of other Kunth species, i.e., of synonymous *V. micrantha* Kunth, or *V. mollis*. Figs. 9–10.

Cacalia bullata (Benth.) Kuntze, *Cacalia canescens* (Kunth) Kuntze, ?*Lepidaploa aristata* Cass., *Vernonia arborescens* var. *cuneifolia* Britton, *Vernonia bullata* Benth., *Vernonia canescens* var. *pilata* S.F. Blake, *Vernonia cuneifolia* (Britton) Gleason, *Vernonia hirsutivena* Gleason, *Vernonia medialis* Standl. & Steyerm., ?*Vernonia micradenia* DC., *Vernonia micrantha* Kunth, *Vernonia patuliflora* Rusby, *Vernonia pseudomollis* Gleason, *Vernonia purpusii* Brandegee, *Vernonia rusbyi* Gleason, *Vernonia sodiroi* Hieron., *Vernonia unillensis* Cuatr., *Vernonia volubilis* Hieron.
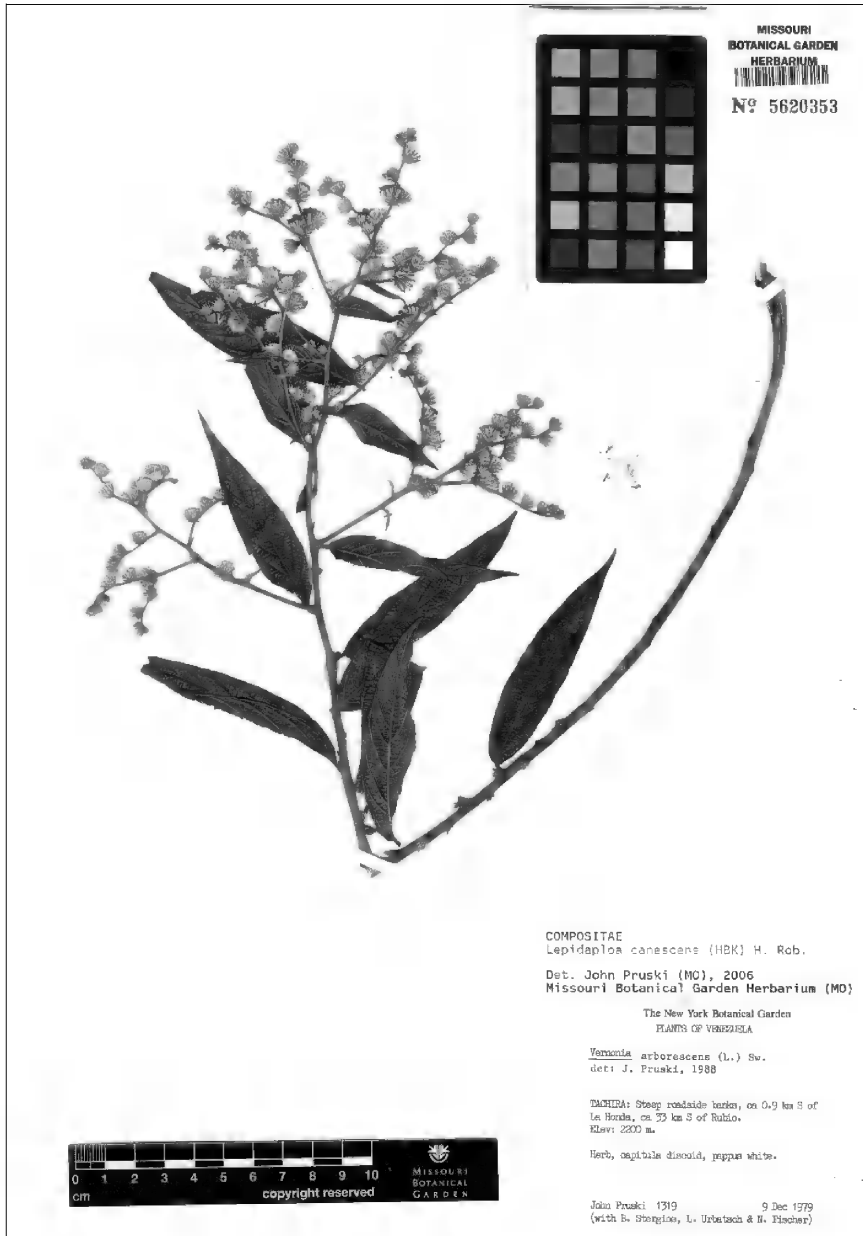
Figure 9.   Representative specimen of *Lepidaploa canescens* showing single capitulescence branch per node, each of which then branches distally.   (*Pruski et al. 1319*, MO).

Subshrubs to shrubs 1–5(–8) m tall; stems erect to scandent, laxly branched, sprawling, subterete, striate distally, villous or densely puberulent, glabrate proximally, leaves usually well-spaced.   **Leaves** alternate, petiolate; blade (3–)5–14(–20) × (1.5–)2.5–5(–7) cm, lanceolate to ovate-elliptic, rarely ovate or oblong, typically broadest in basal third of blade, secondary veins typically 6–11 per side, often impressed adaxially, prominent abaxially, diverging from midrib at about a 50° angle and thereafter strongly arching towards apex, surfaces occasionally slightly discolorous, adaxial surface sometimes rugulose or bullate with secondary veins deeply impressed, eglandular, scabrid with short erect trichomes to substrigose or pilose with elongate trichomes, trichome base sometimes prominent, abaxial surface typically glandular, pilosulose or pilose to densely sericeous, trichomes to ca. 1+ mm long, typically patent-antrorse, base cuneate to broadly obtuse or rounded, margins entire to remotely serrulate, sometimes revolute, apex acute to long-acuminate; petiole 0.3–1.7 cm long, villous.   **Capitulescence** terminal from distal most nodes (very rarely axillary as in type of *V. hirsutivena* but then corolla tube papillose-setulose), typically very well-exserted, non-leafy, of (1–)few–many sparsely but usually repeatedly branched (-simple) seriated cymes (with the sessile capitula moderately well-spaced) typically 4–10 cm long, cymes often arranged in large spreading panicles to 20 × 15 cm, ultimate branchlets with several typically sessile (rarely short-pedunculate) and ebracteolate (seldom inconspicuously linear bracteolate, then typically the bracteate leaf is on the same side of the stem) capitula moderately remote and occurring singly (not in terminal glomerules), branchlets much less commonly shortened with capitula somewhat congested but not in well-defined terminal glomerules.   **Capitula** 5–8 mm long, 18–27-flowered; involucre usually 4–6(–7.5) × 4–5 mm, campanulate; phyllaries 0.5–1 mm diam., 4–6-seriate, graduate, frequently tinged with violet; the outer series 1–2.5 mm long, narrowly lanceolate, somewhat spreading, sericeous to laxly arachnoid-tomentose, these and mid-series phyllaries typically strongly 1-costate to apex, apex typically spinose-aristate; inner series 4–6 mm long, lanceolate, subappressed, sericeous or only apically so, apex occasionally slightly glandular, typically obtuse, frequently short-apiculate, less much commonly aristate.   **Florets** not greatly exserted from involucre; corolla 3.8–5.3 mm long, usually becoming obviously salverform, lavender (rarely white), tube 2.1–2.7 mm long, papillose-setulose or glandular (sometimes subglabrous in *V. medialis*, putative hybrids, and some South America plants), lobes (1–)1.5–2.2 mm long, usually very much longer than the short throat, usually sparsely setose and/or sparsely glandular (sometimes subglabrous in South America); anthers 1.5–2.3 mm long, tails 0.2–0.4 mm long, appendage rarely glandular; style branches 1.5–2.1 mm long. **Cypselae** 1.2–2(–2.5) mm long, turbinate, ribbed, sericeous or strigillose, eglandular but often with resiniferous idioblasts; pappus stramineous to white or dull white, the outer series of fimbriate scales 0.6–1 mm long, the inner series of bristles, usually 3.5–5 mm long. $2n = 32, 34$.

Distribution and Ecology.   *Lepidaploa canescens*, presumably a diploid, is a common Neotropical species that occurs from Mexico and Central America southward to Colombia, Venezuela, Ecuador, Peru, Bolivia, and Brazil.   In Central America is sometimes common enough to form large thickets.   It also occurs on Trinidad and Tobago but not in the Antilles.   The species flowers year-round and in Central America it has been collected from sea level to 2500 meters elevation.

Representative collections.   COSTA RICA.   *Cooper 5839* (MO, US); *Croat 47092* (MO, UC); *Grayum 10482* (MO); *King 6773* (MO, US); *Örsted 4/8540* (C-2 as IDC microfiche 2204 214.II.6–7, one sheet as Macbride neg. 22662, K-BENTH; type of *V. bullata*); *Rodríguez et al. 9762* (MO, NY); *Skutch 3446* (MO, NY, US).   **EL SALVADOR.**   *Calderón 58* (NY, US); *Calderón 1445* (MO, US); *Carlson 37* (F, MO); *Sandoval & Rivera 1481* (B, K, LAGU, MO); *Standley 20301* (NY, US).   **GUATEMALA.**   *Keeley & Keeley 3176* (MO); *King 7241* (NY, US); *King 7250* (MO, NY, US); *Nelson 3691* (F, US); *Skutch 1993* (F, GH, NY, TEX, US; type of *V. canescens* var. *pilata*); *Standley 63945* (F); *Standley 87473* (F; type of *V. medialis*).   **HONDURAS.**   *Clewell 3015* (MO); *Croat & Hannon 63877* (MO, US); *Edwards P-7855* (F, MO, NY, US); *Molina 815* (MO, US);

Williams & Molina 23248 (F, MO, US). **MEXICO. Chiapas**. *Breedlove & Almeda 47686* (CAS, MO); *Matuda 2784* (MEXU, MO, TEX); *Purpus 7189* (MO, NY, UC, US; type of *V. purpusii*); *Ventura & López 2976* (IEB, MEXU, MO, TEX); *Ventura & López 2992* (IEB, MO, XAL). **Quintana Roo**. *Soto et al. 22593* (MO). **Yucatán**. *Gaumer 1325* (F, NY; type of *V. hirsutivena;* cited by Millspaugh and Chase 1904 as *L. arborescens*); *Gaumer 23540* (MO, NY, US). **NICARAGUA**. *Coronado et al. 482* (MO, USM); *Greenman & Greenman 5800* (MO). **PANAMA**. *Allen 187* (MO, US); *Allen 1344* (MO, NY); *Bernal 17* (MO); *Cándido 7* (PMA, MO; axillary flowered but corolla tube setose); *D'Arcy & McPherson 16087* (MO); *Darwin 2831* (MO, NO); *Dwyer et al. 522* (F, GH, K, MO, NY, UC, US); *Fendler 160* (K, MO, US); *Gentry & Mori 13582* (MO, US); *Greenman & Greenman 5202* (MO); *Kennedy 2280* (MO, US); *King 6773* (MO, US); *Nee 9310* (MO, NY); *Standley 29314* (MO, US); *Valdespino 53* (MO, NY, PMA); *Wilbur et al. 13260* (DUKE, MO).

Lepidaploa canescens may be recognized most readily by its typically terminal capitulescence composed of many small sessile capitula with acicular outer phyllaries and narrow-tipped inner phyllaries. It commonly also has broad-based abaxially densely pubescent leaf blades with curved secondary veins. The synonyms *V. canescens* var. *pilata*, *V. medialis*, and *V. hirsutivena* from Guatemala and the Yucatán were named for more weakly pubescent-leaved, axillary capitulate, or larger capitulate populations. Nash (1976) recognized *V. medialis* as distinct, keying it by the nearly double the average involucre size of typical *L. canescens*, but Keeley (1982) reduced *V. medialis* to synonymy with *L. arborescens*. In Central America, *L. canescens* is perhaps most similar *L. lehmannii* (Hieron.) H. Rob., which differs by its capitula consistently clustered at the tips of its branchlets. By terminal capitulescences it is somewhat similar to *L. polypleura*, which otherwise is totally different, arborescent, has larger capitula, obtuse-tipped inner phyllaries, and a (usually) fulvous or tawny pappus.

Blake et al. (1926), Standley (1938), Clewell (1975), Elias (1975), Nash (1976), and McVaugh (1984) recognized *Lepidaploa canescens* (as *Vernonia*) in Central American, but Millspaugh and Chase (1904), Rzedowski and Calderón de Rzedowski (1995), and Turner (2007) cited *L. arborescens* in the Yucatán. Keeley (1982) treated *L. canescens* as a synonym of a broadly defined *L. arborescens*. Recently, Robinson (1990, 1999) recognized *L. arborescens* as a West Indian endemic and referred South American and Central American material to *L. canescens*. Robinson (1990) noted that *L. canescens* usually differs from West Indian material by having larger leaves, smaller involucres, more densely pubescent phyllaries, and by generally lacking capitulescence bracts, or in the infrequent cases when with foliar bracts then these are attached "on the opposite side of the stem" from the capitula (Robinson 1990). Indeed, by its characteristic aphyllous terminal capitulescence *L. canescens* was placed by Gleason (1906; viz also 1923: 195, Fig. 2b) in *Vernonia* sect. *Lepidaploa* "Scorpioideae Aphyllae" nearer to *Vernonanthura patens* than to species now placed in *Lepidaploa*.

Pruski (2010, 2013) applied the name *Lepidaploa canescens* to South American material, which he characterized as typically having usually setose but eglandular corolla lobes. He noted that that Antillean *L. arborescens* has glabrous corolla tubes, densely glandular corolla lobes, and eglandular cypselae often with resiniferous idioblasts. The Mesoamerican (and most South American) material of *L. canescens* has characteristically papillose-setulose or glandular corolla tubes. Some South American materials called *L. canescens* seem to have subglabrous corolla tubes and may belong to cryptic species currently treated in synonymy.

Grayum 10482 has long, simple-flowering seriated-cymose branches resembling those of sympatric *Eirmocephala* H. Rob., but *L. canescens* may be generally diagnosed by corollas with papillose-setulose or glandular tubes and short throats. *Eirmocephala* H. Rob. has broader corollas

with a glabrous tube and a moderately elongate throat. The common widespread *Vernonanthura patens* lacks spinose-aristate outer phyllaries and has leaves abaxially short-strigillose with short, broad, appressed, solid, white, L-shaped trichomes ca. 0.1 mm long but is nevertheless often misdetermined as *L. canescens*.

Figure 10. Protologue illustration of *Vernonia canescens* [≡ *Lepidaploa canescens*] showing the spreading corolla lobes. (Reprinted from Kunth, Nov. Gen. Sp. 4: tab. 317 1820 [1818]).

Many records of *Lepidaploa canescens* from the Yucatán (but not of *Gaumer 1325*, the type of *V. hirsutivena*) may be based on misdeterminations. *Gaumer 23540* from Yucatán has both axillary and subterminal capitula but by papillose-setulose or glandular corolla tubes proves to be *L. canescens* rather than *L. argyropappa*. Cowan (1983) cited *Cowan 1986* and *Cowan 1997* from Tabasco as *L. canescens*, but both are redetermined here as *Vernonanthura patens*, as is material from Campeche as well. Villaseñor (1989: 108) cited *L. canescens* in Tabasco, but it was not cited there by Turner (2007) or by Redonda-Martínez and Villaseñor (2011). The species has apparently not been collected in Belize, albeit cited by Villaseñor (1989) as occurring there.

I am uncertain of the identity of the non-typical variety, Colombian *Lepidaploa canescens* var. *opposita* (H. Rob.) H. Rob., which is provisionally excluded. Thus albeit a segregate of *L. arborescens*, I treat *L. canescens* broadly and without infraspecies. However, in South America the species is admittedly variable as to corolla tube papillosity, and much material there is misdetermined as *L. costata* (Rusby) H. Rob., *L. lehmannii*, and *L. myriocephala* (DC.) H. Rob.

4. **LEPIDAPLOA CHIRIQUIENSIS** (S.C. Keeley) H. Rob., *Phytologia* 78: 385. 1995. *Vernonia chiriquiensis* S.C. Keeley, Brittonia 39: 45, fig. 2. 1987. **TYPE: PANAMA**. Chiriquí, Cerro Hornito, 1400–1750 m, 27 Dec 1977, *Folsom et al. 7212* (holotype: MO; isotypes: BM, MEXU, PMA, US). Fig. 11.

Shrubs 1–2 m tall, sometimes vining; stems glabrous to strigose or hispid. **Leaves** short-petiolate; blade 6–16 × 1.5–3.5 cm, lanceolate to elliptic-lanceolate, chartaceous, secondary veins 5–10 per side, not prominent abaxially, surfaces subglabrous to sparsely substrigillose, both surfaces also pustulate-punctate glandular, base cuneate, margins entire, apex acuminate; petiole 0.6–1 cm long. **Capitulescence** 5–15 cm diam., open corymbiform in Panama and open seriate-cymose in Costa Rica, non-leafy, held above stem leaves; peduncles 0.5–20 mm long. **Capitula** 10–12 mm long, 19–21-flowered; involucre 8–9.5 × 6–8 mm, campanulate; phyllaries 5–6-seriate, extremely strongly graduated, substrigillose to subsericeous more or less throughout, never apiculate or strongly 1-costate; outer phyllaries small to minute, 1–1.8 × ca. 0.6 mm, triangular, apex acute to acuminate, often broadly spreading and slightly decurrent onto peduncle; mid-series and inner series phyllaries with apex obtuse or sometimes with mid-series obtuse and the inner ones broadly acute; inner phyllaries 6–7 × 1–1.5 mm, lanceolate or oblanceolate. **Florets**: corolla 6.5–7.5 mm long, white to pinkish, gradually broad-funnelform or campanulate, glabrous but with cells of tube sometimes bulbous and glistening, tube short, 1–1.5 mm long and never narrowly elongate, throat unusually elongate, about as long as lobes, lobes 2.5–3 mm long; anther thecae ca. 3 mm long, filaments ca. 2.5 mm long; pollen echinolophate; style base nodular. **Cypselae** ca. 2 mm long, ca. 8+ lines of pubescence visible in immature cypselae but otherwise costae not prominent at all when cypselae mature, sericeous (duplex trichome apical cells appressed or sometimes somewhat divergent), eglandular, pericarp raphide crystals ca. 30 µm long, elongate-quadrangular; pappus white or dull white to stramineous, outer squamellae ca. 1 mm long, inner bristles 6–7 mm long and nearly as long as corolla.

Distribution and Ecology. *Lepidaploa chiriquiensis* is a rare southeastern Central American endemic described from Panama but here reported as also occurring in Costa Rica. The species grows in montane forests from 900–2100 meters elevation, flowers from December to March, and has been collected in late fruit in May. In Panama it is known to me to have been collected from 1977–1989 and only from near Chiriquí, but in Costa Rica it is known not only from the somewhat distant Talamanca Mountains near Cerro de la Muerte (a 2001 collection) but also much further to the northwest near Alajuela in the central part of the country, where it was collected in 1982.

Figure 11. Holotype of *Vernonia chiriquiensis* [≡ *Lepidaploa chiriquiensis*] showing the pedunculate capitula and broadly tipped inner phyllaries. A metric ruler is in the upper left of the image. (*Folsom et al. 7212*, MO).

Specimens examined. COSTA RICA. *Carvajal 83* (CR, MO); *Rodríguez et al. 7200* (INB, MO). **PANAMA**. *Hammel 3059* (MO); *Hammel 6194* (MO); *Knapp et al. 4227* (MO); *McPherson 11839* (MO); *McPherson 13561* (MO, US).

By its often pedunculate capitula in open corymbiform capitulescences and its gradually broadening short-tubed long-limbed corollas, *Lepidaploa chiriquiensis* is anomalous in *Lepidaploa*. In other species of *Lepidaploa* where the corolla throats may be about as long as the lobes, the tube is very elongated (e.g., *L. acilepis*, *L. argyropappa*) and the corolla more typical Lepidaploan in its structure. The moderately broad corollas with an elongate throat in *L. chiriquiensis* bring to mind those of *Eirmocephala*. The strange capitulescence form, echinolophate pollen, and slightly decurrent

outer phyllaries are characters shared by *L. chiriquiensis* and several South American species of *Lessingianthus* H. Rob., e.g. Bolivian *L. laurifolius* (DC.) H. Rob.

Some species of *Lessingianthus* are similar to *Lepidaploa* in having elongate-hexagonal pericarp raphide crystals, but most *Lessingianthus* species differ by quadrate raphide-crystals. *Lepidaploa chiriquiensis* has elongate-quadrangular pericarp raphide crystals and does not conflict with either genus. But *L. chiriquiensis* has nodular style bases, a character that conflicts with *Lessingianthus* (viz Robinson 1999, 2007) but which is typical of *Lepidaploa*.

While the two recent collections from Costa Rica have corollas, leaves, and phyllaries typical of *Lepidaploa chiriquiensis*, they have sessile capitula and open seriated-cymose capitulescences atypical of the species but typical of the genus. This suggests that the type material from Panama may actually be atypical of the species and conversely that the newly detected Costa Rican populations could be the most characteristic *Lepidaploa* form.

As part of ongoing studies, further material of *Lepidaploa chiriquiensis* from Costa Rica and Panama will be sought, which when in hand I anticipate could help show trends in morphological variation, phylogenetic affinities, and may shine light towards its correct generic placement. Given the paucity of collections (and inconclusive micromorphology), *L. chiriquiensis* seems best retained at present in *Lepidaploa*, albeit atypical there.

5. **LEPIDAPLOA LEHMANNII** (Hieron.) H. Rob., Proc. Biol. Soc. Washington 103: 489. 1990. *Vernonia lehmannii* Hieron., Bot. Jahrb. Syst. 19: 44. 1894. **TYPE: COLOMBIA. Cundinamarca.** Prope Pacho, 1600–2200 m, Jan 1892, *Lehmann 7482* (holotype: B†, Macbride neg. 14557; lectotype (designated here): US-1420448; isotypes: F, K n.v., S). The handwriting style of Hieronymus on the B sheet is not a perfect match for the handwriting on either the F, S, or US sheets, which Hieronymus may not have seen, but nevertheless the US lectotype matches *Lepidaploa lehmannii* as applied currently. Fig. 12.

Cacalia lehmannii (Hieron.) Kuntze, *Vernonia larensis* V.M. Badillo

Shrubs to vines 1–7 m tall; stems erect to scandent or sprawling, subterete, striate distally, crisped puberulent to griseous villous-pilose. **Leaves** alternate, short-petiolate; blade 5–13 × 2–3.5 cm, lanceolate to ovate-lanceolate, secondary veins typically 5–6(–8) per side, sometimes impressed adaxially, moderately prominent abaxially, moderately arching towards apex, surfaces concolorous, adaxial surface smooth or sometimes rugulose, eglandular, strigillose to subglabrous, abaxial surface glandular, hirtellous-pilose to strigillose, base cuneate to obtuse(–rounded), margins entire, sometimes revolute, apex narrowly acute to long-attenuate; petiole 0.2–0.6 cm long, hirtellous. **Capitulescence** terminal on short lateral branchlets from distal most nodes, somewhat exserted, non-leafy and ebracteolate, of few–several densely-capitulate, densely branched seriate-cymes typically 3–7 cm long, cymes arranged in tightly held panicles at apex of main stems, ultimate branchlets with several small capitula subglomerate at apex, sometimes longer branchlets less compact-capitulate proximal to apex, then with a very few capitula occurring singly and ca. 0.5 cm from each other. **Capitula** 6–8 mm long, (13–)19–23-flowered; involucre usually 4–5.5 × 3–4.5 mm, campanulate, without outer elongate acicular phyllaries; phyllaries 4–5-seriate, strongly graduate, strigillose to villous; the outer series 1–1.5 × ca. 0.5 mm, narrowly lanceolate, appressed, these and mid-series phyllaries moderately 1-costate towards apex, but apex not obviously long-aristate at all; inner series 4–5 × ca. 1 mm, lanceolate, appressed, typically broadly acute to subobtuse, slightly apiculate. **Florets** exserted from involucre; corolla 3.8–6 mm long, becoming salverform, lavender to violet, glabrous or lobe apex few-glandular, tube 2–3 mm long, glabrous, throat short, lobes 1.5–2 mm long, longer than the throat, usually lightly glandular; anthers ca. 2 mm long, often fully exserted.

Cypselae 1–2 mm long, turbinate, ribbed, sericeous, eglandular; pappus white or dull white, the outer series of fimbriate scales 1–1.5 mm long, the inner series of bristles 4–4.5 mm long.

Figure 12. Lectotype of *Vernonia lehmannii* Hieron. showing branchlets tips subglomerate-flowered. [≡ *Lepidaploa lehmannii* (Hieron.) H. Rob.]. (*Lehmann 7482*, US).

Distribution and ecology. *Lepidaploa lehmannii* is a new record for Central America (not reported in Panama by Pruski 2013) and the species is now known in Panama, Colombia, Venezuela, and Ecuador. It is known in Central America only from a single collection made in Panama along the

border with Choco, Colombia, where it was collected as a vine over branches in a primary forest at 850 meters elevation, flowering in October.

Collection examined. PANAMA. Darién. Parque Nacional del Darién, ridge between Río Topalisa and Río Pucuro, ca. 17 km E of Pucuro, La Laguna area, 08° 03' 30" N, 77° 17' 00" W, 850 m, 16 Oct 1987, *de Nevers, Cuadros, Hammel & Herrera 8371* (MO, US).

The Klatt (1886) treatment of Lehmann collections mentioned only three collections but not the type collection of our species, which post-dated the Klatt work. Although Klatt was still publishing his treatments for Florae Costaricensis (viz Klatt 1892, 1896), by 1892 when the *L. lehmannii* type was collected Klatt was in his mid-60s, and determinations of Lehmann Compositae mostly fell into the hands of Hieronymus (viz Hieronymus 1894, 1901), who was 21 years Klatt's junior.

Lepidaploa lehmannii has been moderately well collected in South America. Pruski and Funston (2011) noted *L. lehmannii* to be moderately widespread in Antioquia Colombia, occurring there from near sea level to 2500+ meters elevation. Thus, the 1987 collection along the Choco-Darién frontier was a to-be-expected minor range extension. The species is similar to *L. canescens* but differs by sparser short leaf pubescence, dense terminal cymes, glabrous corolla tubes, and a relatively long outer series of pappus scales.

6. **LEPIDAPLOA POLYPLEURA** (S.F. Blake) H. Rob., *Smithsonian Contr. Bot.* 89: 72. 1999. *Vernonia polypleura* S.F. Blake, *J. Wash. Acad. Sci.* 28: 478. 1938. **TYPE: MEXICO. Chiapas**. Mt. Orando [possibly on labels in error for Ovando], 23 Dec 1936, *Matuda 730* (holotype: US; isotypes: MEXU, MICH, TEX). Figs. 13–14.

Shrubs to trees 3–19 m tall; stems densely tomentulose to tomentose, trichomes patent, mostly 0.2–0.4 mm long, distal internodes much shorter than leaves. **Leaves** petiolate; blade 10–22 × 2–5–7.5 cm, lanceolate or elliptic-lanceolate to oblanceolate or rarely obovate, typically broadest near middle of blade, stiff-chartaceous, secondary veins 8–12(–17) per side, prominent abaxially, diverging from midrib at about 45° then near margins becoming arcuate, adaxial surface eglandular, pilose-hirsute to only so on veins with areolae subglabrous, trichomes patent or subappressed, often deciduous above prominulous base, abaxial surface (moderately–) densely pilose-villous to tomentose, also glandular, base acuminate, margins entire or subentire, apex acute to acuminate; petiole 1–3 cm long. **Capitulescence** terminal, non-leafy, held above stem leaves (infrequently a few proximal capitula bracteate), seriate-cymose or a diffuse panicle, capitula usually 1–1.5(–2) cm apart, sessile, ultimate branches relatively (5–25 cm) long, densely tomentulose. **Capitula** 7–10 mm long, 17–25-flowered; involucre 6–7 × 5–8 mm, campanulate, sometimes subtended by a pilose-tomentose bracteole 0.2–0.8 cm long; phyllaries graduated, 5–6(–7)-seriate, erect, villosulous to strigillose-sericeous; outer series 1–2 × ca. 0.5 mm, triangular-lanceolate, apex acute to acuminate but never long-subulate; mid-series and inner series with apex usually obtuse to rounded, albeit often mucronulate; inner series 6–7 × 0.8–1.3 mm, elliptic-lanceolate, sometimes slightly constricted below the relatively broad apex. **Florets**: corolla 5–6 mm long, broadly funnelform, pink to lavender (rarely white), tube relatively short, glabrous, limb and especially lobes obviously setose, lobes ca. 2 mm long. **Cypselae** 1.6–2.5 mm long, substrigose, eglandular; pappus commonly fulvous or tawny, infrequently stramineous; outer squamellae 0.5–0.8 mm long; inner bristles 4–5 mm long.

Distribution and ecology. *Lepidaploa polypleura* was known previously from only southern Mexico (Chiapas and Oaxaca) and Guatemala, but is newly reported in (P.N. Montecristo in extreme NW) El Salvador and (west-central) Honduras from woody, angle-stemmed specimens, albeit each

imperfect. The species is occasional and has been collected at about (700–)1300–2400 meters elevation, in flower from December to March.
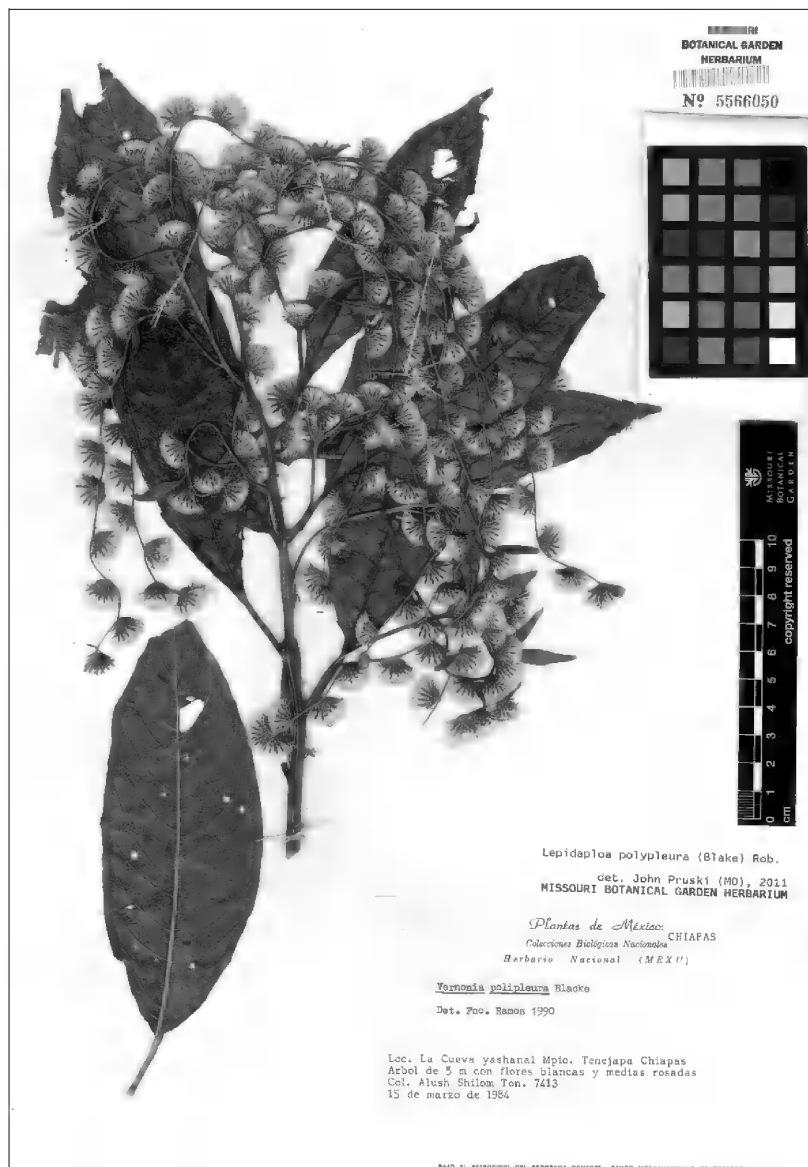
Figure 13. Representative specimen of *Lepidaploa polypleura* showing the pluriveined leaves and terminal capitulescence. (*Shilom Ton 7413*, MO).
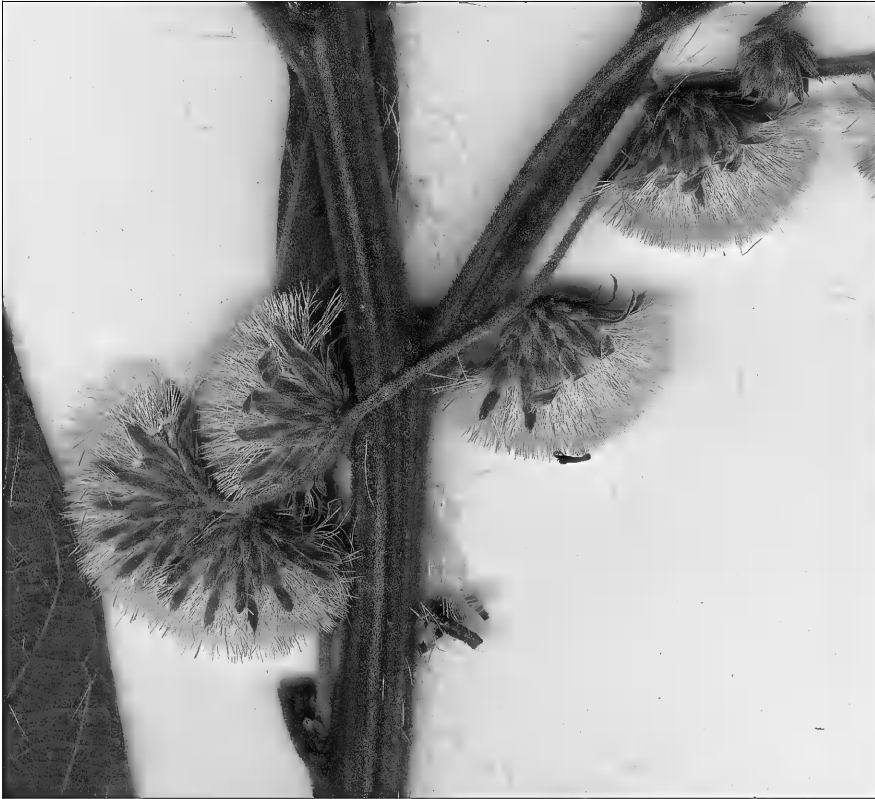
Figure 14. Close-up of *Lepidaploa polypleura* from figure 13 showing the angled-stems, tawny pappus bristles, and relatively broad-tipped phyllaries. (*Shilom Ton 7413*, MO).

Representative specimens. EL SALVADOR. *Martínez 528* (MO). **GUATEMALA.** *Rodríguez 433* (P, US). **HONDURAS.** *Evans 1116* (MO). **MEXICO. Chiapas**. *Breedlove 24117* (CAS, MO); *Breedlove 33475* (CAS, MO); *Breedlove & Almeda 58096* (CAS, MEXU, MO, TEX); *Breedlove & Almeda 58310* (CAS, MEXU, MO); *Croat 47629* (MO, UC); *N. Martínez 1432* (HEM, MO); *Matuda 2067* (MEXU, US); *Shilom Ton 7413* (IEB, MEXU, MO); *Stafford et al. 331* (BM, MEXU, MO; 20-flowered but pappus paler than usual). **Oaxaca.** *Maya 4198* (MEXU, MO, TEX).

Lepidaploa polypleura may be recognized by its woody habit, angled stems, relatively narrow leaf blades with several–many prominent secondary veins, terminal capitulescences, broad-tipped inner phyllaries, broad hairy corollas, and its fulvous or tawny pappus. It is quite distinctive among Central American species and brings to mind Colombian *L. cordiifolia* (Kunth) H. Rob., which seems to differ by acute mid-series and inner phyllaries and by a more densely branched capitulescence with much short terminal branchlets. The fine illustration of *L. polypleura* provided by Redonda-Martínez and Villaseñor (2011) shows the characteristic long narrow leaf blades with many prominent secondary veins but depicts the mid-series phyllaries as much more acute than usual. The narrower tipped mid-series condition is found only occasionally in material from Oaxaca.

By similar elongate leaf trichomes and terminal capitulescences, Robinson (1990) reduced *L. polypleura* to synonymy with *L. canescens*, but Robinson (1999) reinstated the species. Nash (1976), Redonda-Martínez and Villaseñor (2011), and Pruski (2013) also recognized the species as distinct. Turner (2007) recognized *L. polypleura* as endemic to Chiapas and Guatemala, but Redonda-Martínez and Villaseñor (2011) and Pruski (2013) noted its occurrence also in Oaxaca.

The single specimen seen from Honduras was described by the collector as white-flowered, and indeed in the dried specimen in front of me not only are the corollas pale but the pappus is much lighter in color than other collections seen. By the stems, leaves, terminal capitulescence, and setose corolla lobes, however, this collections matches the species. The single specimen seen from El Salvador is in bud (but labeled as white-flowered) but similarly is woody and has angled stems. These pale-pappose(-flowered) plants (from El Salvador, Honduras, and *Stafford et al. 331* from Chiapas) are fairly pubescent-leaved and ca. 20-flowered but nevertheless recall partly sympatric *L. tenella*, a similar albeit much less pubescent, few-flowered relative.

7. LEPIDAPLOA TENELLA (D.L. Nash) H. Rob., *Proc. Biol. Soc. Wash.* 1032: 495. 1990. *Vernonia tenella* D.L. Nash, *Fieldiana, Bot.* 369: 74. 1974. TYPE: **GUATEMALA. San Marcos**. Tajumulco Volcano, 8–10 km W San Marcos, 2300 m, 31 Dec 1964–1 Jan 1965, *Williams et al. 26876* (holotype: F).

Lepidaploa boquerona (B.L. Turner) H. Rob., *Vernonia boquerona* B.L. Turner

Shrubs or vines 2–3 m tall; stems arching to scandent, subterete, striate, puberulent to substrigillose or glabrate, trichomes often appressed, distal internodes about 1/2 as long as leaves. **Leaves** petiolate; blade 5–12 × 1.5–3 cm, lanceolate to ovate-lanceolate, broadest near the middle, chartaceous, secondary veins usually 5–7 per side, adaxial surface smooth or sometimes veins somewhat impressed, prominulous abaxially, diverging from midrib at about 45°, surfaces eglandular, adaxial surface glabrous or costa puberulent, abaxial surface puberulent especially on the veins, never densely tomentose, base narrowly cuneate to attenuate, margins entire, apex acute to acuminate; petiole 0.3–1.5 cm long. **Capitulescence** a terminal non-leafy diffuse panicle with individual branchlets seriate-cymose, capitula usually 1–2 cm apart, sessile, ultimate branches 5–10 cm long, appressed-pubescent to tomentulose. **Capitula** 8–10 mm long, 8–15-flowered; involucre 6–8 mm long, turbinate-campanulate or campanulate, sometimes subtended by a reduced bracteole; phyllaries moderately to strongly graduated, 4–5(–8)-seriate, erect, villosulous to strigose-sericeous; outer series 1–2 × ca. 0.5 mm, triangular-lanceolate, never acicular, apex acute to acuminate but never long-subulate; inner series 6–8 × 0.9–1.3 mm, lanceolate or oblanceolate, apex obtuse or sometimes acute. **Florets** slightly exserted or in fruit well-exserted; corolla 6–7 mm long, somewhat broadly funnelform, purplish, lobes 2–3 mm long, setose. **Cypselae** 2–3 mm long, substrigose or pilose; pappus white or dull white; outer squamellae ca. 1 mm; inner bristles ca. 6 mm long.

Distribution and Ecology. *Lepidaploa tenella* is a rare montane (pine or oak) forest shrub endemic to Guatemala (San Marcos in the southwest) and Mexico (southernmost Chiapas) and occurs only near Volcán Tacaná, Volcán Tajumulco, and the Sierra Madre on the Pacific watershed. It has been collected from about 1800–2600 meters elevation and flowers between November and January. Both Turner (2007) and Redonda-Martínez and Villaseñor (2011) used the name *L. boquerona* for our species. *Lepidaploa tenella* was described and long-known from only Guatemala, but here *L. boquerona* is treated in synonymy with *L. tenella*, which is consequently a new record for Mexico. The respective type localities, albeit each in a different country, are only 60 km distant from each other.

Representative specimens. GUATEMALA. *Williams et al. 26094* (F, NY); *Williams et al. 26246* (F, US). **MEXICO. Chiapas**. *Breedlove 42791* (MEXU); *Breedlove & Sigg 66118* (CAS, MEXU, TEX); *Breedlove & Sigg 66139* (CAS; type of *V. boquerona*).

Pruski (2013) keyed *Lepidaploa boquerona* as 8–9-flowered and *L. tenella* as ca. 15-flowered, but further study has convinced me that these two weakly pubescent plants are a single species. *Lepidaploa boquerona* is thus reduced to synonymy with *L. tenella*. By similar terminal capitulescences, broad-tipped phyllaries, and setose corolla lobes, *L. tenella* is envisioned as a subglabrous to less densely pubescent-leaved, fewer-flowered, and paler-pappose relative of *L. polypleura*. But the two species seem sufficiently distinct and each is recognized. The occasional plants that are pale-pappose and have abaxially merely moderately pilose-villous leaves, thus especially recalling *L. tenella* (e.g., *Stafford et al. 331* from Chiapas), are ca. 20-flowered and referred, albeit with some reservations, to the much more common *L. polypleura*. The aspect of *L. tenella* much resembles that of *Vernonanthura patens* (Kunth) H. Rob., a common widespread neotropical weed characterized by its strange, solidm small trichomes (?T-shaped) on its abaxial leaf surfaces.

8. LEPIDAPLOA TORTUOSA (L.) H. Rob., *Proc. Biol. Soc. Wash.* 103: 495. 1990. *Conyza tortuosa* L., *Sp. Pl.* 862. 1753. **LECTOTYPE**: (designated by Britten 1898): **MEXICO.** Veracruz, *Houstoun s.n.* (BM-CLIFF 405 *Conyza* 5). Figs. 2–3, 15–16.

Cacalia schiedeana (Less.) Kuntze, *Cacalia seemanniana* (Steetz) Kuntze, *Conyza scandens* Mill., *Vernonia schiedeana* Less., *Vernonia seemanniana* Steetz, *Vernonia tortuosa* (L.) S.F. Blake, *Vernonia vernicosa* var. *comosa* Greenm.

Shrubs 1–5 m tall; stems usually scandent or climbing, striate, villosulous or pilosulose to more typically densely tomentulose (rarely glabrous). **Leaves** petiolate or short-petiolate; blade (5–)8–17 × 2–6(–9.5) cm, elliptic-lanceolate to ovate, stiffly chartaceous, secondary veins usually prominent, 6–10 per side, spreading to slightly ascending, adaxial surface strigillose or hirsute throughout or at least along proximal portion of midrib, veins sometimes impressed, abaxial surface weakly sericeous or strigillose to villous-tomentose, not glabrous, trichomes mostly 0.1–0.5 mm long, patent to appressed, sometimes also slightly glandular, base cuneate to rounded (rarely subcordate), margins usually entire, sometimes subrevolute, apex acuminate to broadly obtuse; petiole 0.3–1.6 cm long, often tomentulose. **Capitulescence** of bracteate-leafy seriate-cymes to weakly leafy freely branched panicles with ultimate paniculate branchlets usually 7–15 cm long, capitula remotely spaced (internodes 1–4 cm long), sessile or subsessile, bracteate leaves similar to vegetative leaves but much smaller; peduncles 0–2(–3) mm long. **Capitula** (9–)11–15 mm long, (18–)25–40(–50)-flowered; involucre (7–)9–12 × (5–)7–11 mm, campanulate; phyllaries strongly graduate (rarely merely moderately graduate in specimens from Olancho, Honduras), 5–8(–10)-seriate, dull-green tinted distally or inner ones pale brown, substrigillose or subsericeous medially in mid-series, in bud covered by dense arachnoid pubescence mostly derived from cilia from the distal mid-series and inner series phyllary margins; outer phyllaries spreading; outer and mid-series phyllaries 1–6 × 0.5–1.5 mm, triangular to lanceolate, midrib thick and raised in distal 1/2–1/3, apex gradually and stoutly cuspidate; inner 1–2 series of phyllaries (6–)8–12 × 2–3 mm, oblanceolate to oblong, nerves indistinct, margins often distally villous-ciliate, apex typically constricted then distally dilated and cucullate, usually membranous-scarious, obtuse to rounded, clinanthium to 6 mm diam., usually flat. **Florets**: corolla (6–)8–11 mm long, relatively narrowly funnelform becoming slightly salverform, often widely spreading laterally from top of the involucre, white, infrequently faint violet, usually glabrous throughout or lobes sometimes setulose or glandular, tube and limb nearly subequal, throat very short, lobes (2.2–)3.5–4 mm long, often fully exserted from involucre; anther thecae longer than filaments, nearly as long as corolla lobes. **Cypselae** (1.5–)2–2.5 mm long, densely substrigose to

hirsutulous, eglandular; pappus white or dull white to stramineous, outer squamellae 1–2 mm long, inner bristles (5–)6–8 mm long, reaching to about top of involucre and to about base of corolla lobes.

Figure 15. *Lepidaploa tortuosa*. Sessé and Mociño expedition illustration labeled in Candolle's hand as the non-published *Conyza? secunda*. The faint number "19-1" on the upper portion of the plate refers to the Linnaean sexual system Class XIX Syngenesia: Polygamia Aequalis. Neither the species nor this illustration appears to be cited in either Sessé and Mociño (1887) or McVaugh (1980, 2000). In the Madrid Herbarium I find one sheet only of *Lepidaploa tortuosa*: Sessé & Mociño 4147 (Field neg. 42898, IDC microfiche BT-13 card 267-A4) originally labeled as "dubia." This figure was drawn between 1787–1803 and is figure 1045 in the Torner collection (Illustr. Hunt Institute (Torner) 6331.1045).

Distribution and Ecology. *Lepidaploa tortuosa* is widespread, occurring from southern Mexico southeastwards into Panama. The species flowers mostly in (November–)December–April(–August) from sea level to 1900 meters elevation. There is a general north-south trend not taken by me as taxonomically significant, from Mexican plants with very broad phyllaries and eglandular long-pubescent leaves to Panamanian plants with narrower phyllaries and glandular short-pubescent leaves. In Panama, *L. chiriquiensis* has glandular short-pubescent leaves and is similar (to the type of *V. seemanniana*) but lacks spinose phyllaries.

Representative specimens. BELIZE. *Arvigo et al. 122* (MO, NY, US); *Bartlett 12885* (MO, US); *Davidse & Brant 32375* (LP, MO, US); *Gentle 1920* (MICH, MO, NY); *Proctor 35807* (IJ, MO); *Schipp 12* (MO, NY, US). **COSTA RICA.** *Davidse et al. 23364* (MO, US); *Dodge & Thomas 6284* (MO, US); *Morales et al. 1234* (INB, MO); *Pittier 3727* (US; cited by Klatt 1892: 184 as *Vernonia schiedeana*); *Rodríguez et al. 3399* (INB, MO); *Skutch 4112* (MO, US); *Williams et al. 24221* (F, MO); *Williams et al. 26474* (MO, US). **EL SALVADOR.** *Calderón 1509* (NY, US); *Carbollo et al. 1124* (B, LAGU, MO); *Munro et al. 2275* (B, BM, LAGU, MO); *Standley 19992* (MO, US). **GUATEMALA.** *Blake 7712* (US); *Contreras 726* (MO, TEX, US); *Contreras 3478* (MO, TEX, US); *Tuerckheim 1346* (MO, US); *Türckheim II 1627* (MO, US). **HONDURAS.** *Blackmore & Heath 2146* (BM, MO); *Croat & Hannon 64287*(MO, US); *Evans 1344* (EAP, MO, NO, UC); *Nelson & Clewell 404* (MO); *Nelson & Vargas 2674* (MO); *Thieme 5307* (US); *Williams & Molina 17943* (US). **MEXICO. Campeche.** *Flores 10428* (CICY n.v.; cited by Redonda-Martínez and Villaseñor 2011). **Chiapas.** *Breedlove 50441* (CAS, MO, TEX); *Croat 47502* (MEXU, MO; cited by Redonda-Martínez and Villaseñor 2011 as *L. remotiflora*); *Matuda 736* (MEXU, MO); *Pruski et al. 4191* (HEM, K, MEXU, MO, TEX, UC); *Pruski et al. 4239* (HEM, MO); *Ventura 880* (MEXU, MO, XAL). **Tabasco.** *Cowan 2772* (CAS, MEXU, MO, NY, TEX); *Cowan 2800* (CAS, ENCB, MEXU, MO, NY); *Fernández 1430* (IEB, MO); *Johnson 15* (K). **Veracruz.** *Houstoun s.n.* (BM-Banks (NYBG neg. 577, BH neg. 5224), BM-Sloane 292, 65/67 [sic]; type of *Conyza scandens*); *Pruski & Ortiz 4125* (GH, K, MEXU, MO, NY, TEX, UC, XAL; distributed as *Vernonia patens*); *Schiede 1237* (HAL-2; type of *V. schiedeana*). **NICARAGUA.** *Araquistain & Moreno 1748b* (MO); *Nelson 4914* (BM, F, GH, MO); *Pipoly 4430* (MO). **PANAMA.** *Allen 4179* (MO); *Folsom 15997* (MO); *Hamilton & Dressler 2993* (MO, UC); *Seemann 1589* (BM, K-Hook; type of *V. seemanniana*); *Sytsma 4040* (MO, US).

The common and widespread *Lepidaploa tortuosa* can be recognized by its moderately large axillary capitula, an arachnoid involucre in bud, and pubescent phyllaries, the inner series of which are dilated distally and broad-tipped at apex. Only in few areas with steep rocky river banks in Olancho, Honduras, is the involucre arachnoid-pubescent but with acute inner phyllaries and outer phyllaries strongly spreading-decurrent onto peduncle (e.g., *Blackmore & Heath 2146; Croat & Hannon 64287; Nelson & Vargas 2674*), which I suspect are ecological variants.

Gleason (1922) recognized each *Vernonia schiedeana*, *V. seemanniana*, and *V. vernicosa* as distinct, but Blake (1926) recognized *V. tortuosa* and placed *V. schiedeana* in synonym of it. Elias (1975) recognized *V. seemanniana* in Panama and Standley (1938) recognized *L. vernicosa* in Costa Rica as distinct. Robinson (1999) expanded Blake's synonymy by also treating *V. seemanniana* and *V. vernicosa* in synonymy with *L. tortuosa*. As circumscribed by Robinson (1999), *L. tortuosa* is broadly defined but here slightly less broadly so with *L. vernicosa* reinstated below and circumscribed more or less as in Gleason (1906, 1922). As circumscribed here, there is in *L. tortuosa* a distinct (but not absolute) trend from northern populations (the typical forms) often having hairier leaves and broad-tipped nearly cucullate inner phyllaries to southern populations (described as *Vernonia seemanniana*) in Costa Rica and Panama often having more weakly pubescent but glandular leaves and narrow-tipped inner phyllaries.

Figure 16. Representative specimen of *Lepidaploa tortuosa* showing the leafy capitulescence with large axillary capitula. (*Pruski et al. 4239*, MO).

   The citation by Hemsley (1881: 74) of *Vernonia schiedeana* in "Yucatan and Tabasco" vouchered by *Johnson 15* (K) is in reference to a collection I presume to be from Tabasco. I know of no Johnson collections from Edo. Yucatán, where this species remains undocumented.

9. LEPIDAPLOA UNIFLORA (Mill.) H. Rob., Proc. Biol. Soc. Wash. 103: 496. 1990. *Conyza uniflora* Mill., Gard. Dict. (ed. 8), *Conyza* no. 13. 1768. **LECTOTYPE** (designated here): **MEXICO**. ?Campeche, *Anon.,* possibly *Houstoun* (lectotype: BM-*Conyza Americana frutescens …* (BH negative 5226, as photograph in E, MO, NY). Possible syntype or possible isolectotype: BM-Sloane vol. 5 sheet 17, specimen on right. The lectotype contains the Houstoun binomial cited in the protologue by Miller (1768), and is presumably a Houstoun sheet collected pre-1733 (the year Houstoun died in Jamaica). The protologue (as Conyza no. 13) included the Houstoun polynomial, and also mentioned other materials coming from the same source as Conyza no. 12, i.e., "from Carthagena …. Mr. Robert Millar." Blake (1915) gave the Millar material as collected about 1736. Although the lectotype may be a Houstoun collection, the species is unknown in Veracruz, where most Houstoun material originated. The Millar locality "Carthagena" is possibly in reference to Cartago, Costa Rica [Blake 1915 stated that Millar's Carthagena to "eighteenth century collectors … is … Cartago, not Carthagena, Columbia"], but the species is not known from either Costa Rica or Colombia either. If indeed original material was received by Philip Miller from Robert Millar, most likely the actual locality is instead "Campeachy" from where some Millar material originates and from where the species is known. The Sloane herbarium sheet is not clearly the same collection as the lectotype sheet, and perhaps instead it is the Robert Millar syntype material. The BM Sloane herbarium sheet from folio 5 is a later continental American addition to the otherwise mostly West Indian folios 1–7, and Houstoun collections are occasional in the Sloane folios (Dandy 1958). Fig.17.

Cacalia uniflora (Mill.) Kuntze, non Schumach. & Thonn., *Vernonia ctenophora* Gleason

Perennial herbs 1–1.5(–2) m tall, apparently brittle-stemmed and sometimes labeled as a shrub, but perhaps never truly woody based; stems few-branched, weakly striatulate distally, villosulous, also glandular. **Leaves** short-petiolate; blade 2.5–5.5 × 0.8–2.5 cm, lanceolate to elliptic-lanceolate (widest below the middle), chartaceous, secondary veins 4–6 per side, both surfaces glandular, adaxial surface also thinly and sparsely villosulous-strigillose, smooth, abaxial surface villosulous-strigillose to villous-strigose with antrorse, sometimes griseous trichomes to ca. 0.5 mm long, base rounded or obtuse, margins entire, apex acuminate; petiole 0.1–0.4 cm long. **Capitulescence** leafy, with a single sessile axillary capitulum (whence the epithet) in each of the 5–10+ distal well-spaced nodes, the capitula remote but nevertheless the arching branch tips often more or less unifacial and thus loosely seriate-cymose, branches sometimes pressing very weakly bifacial and fractiflex. **Capitula** 7–10 mm long, 18–23-flowered; involucre 6–7(–8) × 4–6(–7) mm, turbinate to campanulate, reaching to about base of corolla lobes; phyllaries graduate or sometimes weakly graduate with outer phyllaries more than half as long as the inner, 0.2–1.5 mm diam., substrigillose to subsericeous and glandular distally, ca. 4-seriate; outer 1–2 series of phyllaries linear-lanceolate, 1-costate distally, apex long-subulate with apical mucro 1–2 mm; the mid-series often abruptly cuspidate and purplish in the middle; inner 1–2 series of phyllaries elliptic-lanceolate, purplish distally, apex acuminate. **Florets**: corolla 6–7 mm long, tubular-funnelform, reddish to pinkish, tube glabrous, slightly longer to much longer than limb, throat short, lobes ca. 2.5 mm long, sparsely to moderately setose distally to sometimes proximally to near throat, glandular distally. **Cypselae** 1.3–1.5 mm long, strigillose, intercostae glandular; pappus outer squamellae 0.6–1 mm long, inner bristles 4–5 mm long, reaching to proximal 1/3 of corolla lobes.

Distribution and Ecology. *Lepidaploa uniflora* is basically a Yucatán peninsula endemic –– Belize, Guatemala (Petén), and Yucatán peninsular Mexico –– where it is moderately common and occurs in and near open low forest, pastizal, and tintal from 10–300 meters elevation, flowering mostly from November to May.

Figure 17. Representative specimen of *Lepidaploa uniflora*. (*Lundell 1221*, MO).

Representative collections.   **BELIZE.**   *Bartlett 11530* (US); *Davidse & Brant 32784* (MEXU, MO, NY); *Davidse & Brant 32829* (BM, MO, US). **GUATEMALA**. *Contreras 484* (MO,

US); *Contreras 8545* (MO, US). **MEXICO. Campeche**. *Goldman 508* (US; holotype of *V. ctenophora*); *Lundell 1221* (MO, US; cited by Martínez et al. 2001 as *L. argyropappa*; cited by Carnevali et al. 2010 as *L. salzmannii*); *Martínez et al. 2955* (CICY, IEB, MEXU, MO). **Quintana Roo**. *Cabrera 1277* (MEXU; cited by Sousa and Cabrera 1983 as *L. argyropappa*; cited by Carnevali et al. 2010 as *L. salzmannii*); *Carnevali et al. 5437* (CICY, MEXU, MO); *Hernández 303* (CICY, MO). **Tabasco**. *Fernández & Guadarrama-Zamudio 1336* (MO); *Matuda 3112* (MEXU, MICH, MO; cited by Cowan 1983 as *V. ctenophora*).

Lepidaploa uniflora may be recognized by its obviously glandular cypselae, leaf blades glandular on both surfaces, and tubular-funnelform (not as drawn in Redonda-Martínez and Villaseñor 2011, where all species are depicted as similarly salverform). *Lepidaploa uniflora* was recognized by Nash (1976), Villaseñor (1989), and Turner (2007) as *V. ctenophora* Gleason. Pruski (2016) noted that *Vernonia uniflora* Sch. Bip. blocked use of the Miller name in *Vernonia*. The plant was called *L. uniflora* by Robinson (1990, 1999), Redonda-Martínez and Villaseñor (2011), and Pruski (2013). By the unusual characters of strongly glandular cypselae and leaves obviously glandular adaxially, *L. uniflora* is reminiscent of Guayana Highland endemic *L. bolivarensis* (V.M. Badillo) H. Rob. (Pruski 1997). The report by Carnevali et al. (2010) of *L. uniflora* in Chiapas is apparently based on a misdetermination. Redonda-Martínez and Villaseñor (2011) erroneously gave Brazilian *Lessingianthus varroniifolius* (DC.) H. Rob. in synonymy with *L. uniflora*. Britten (1898) and Aristeguieta (1964) gave *Conyza uniflora* in synonymy with similarly aristate-phyllaried *V. remotiflora* Rich., which in the strict sense is South American and has narrower capitula. Pruski (2016) recognized *L. uniflora* as one of six Miller (1768) species described in *Conyza*. Miller (1768) described well the axillary capitula, but (mis)stated that the plant is "eight or ten feet high," whereas material I have seen is herbaceous and less than 1.5(–2) meters tall.

10. **LEPIDAPLOA VERNICOSA** (Klatt) Pruski, **comb. nov.** *Vernonia vernicosa* Klatt, Bull. Soc. Roy. Bot. Belgique 35(1): 294. 1896. **TYPE: COSTA RICA**. Bord du Río Virilla, Jan 1896, *Tonduz 7065 [= 9860 herb. nat. Cost.]* (holotype: BR; isotypes: CR, F, GH p.p., MO, US). The BR sheet is complete, but a fragment of it is on the left of the GH sheet. Figs. 18–19.

Vernonia vernicosa var. *comosa* Greenm.

Shrubs, sometimes vines 0.3–3 m tall; stems erect to scandent, striate, glabrous to puberulent. **Leaves** blade 3–11 × 1–4 cm, lanceolate to ovate-lanceolate, chartaceous, secondary veins thin, usually 3–5 per side, directed forward, adaxial surface smooth and sometimes nitidous, veins sometimes weakly impressed, glabrous to strigillose, trichomes (when present) appressed, sometimes punctate, abaxial surface weakly strigose, trichomes mostly 0.1–0.3 mm long, appressed, also glandular, base broadly obtuse or rounded to rarely subcordate, margins entire, apex acute to attenuate; petiole 0.3–0.4 cm long, glabrous to puberulent. **Capitulescence** of lax sparsely branched leafy elongate branches (taking up much of individual herbarium sheets) with large axillary capitula solitary in distal nodes, flowering branchlets nodally deflected-fractiflex distally (not obviously seriate-cymose), capitula remote, well-spaced, nodes 2–5 cm long, subsessile to very short-pedunculate, bracteate leaves similar to vegetative leaves but slightly smaller; peduncles to 3 mm long. **Capitula** 12–18 mm long, 50–62+-flowered; involucre 10–14 × 9–12 mm, campanulate; phyllaries strongly graduate, all gradually narrow-acuminate or sometimes the mid-series broader and abruptly narrowed apically from broad apex, 7–9-seriate, outer and mid-series stiff-coriaceous nitidous green distally with pale midrib and pale very thin margins, grading to inner ones thin and pale brown in distal 1/3, glabrous to sometimes minutely and weakly puberulent or ciliate, in bud all phyllaries glabrous or mid-series loosely arachnoid pubescent; outer phyllaries 2–5 × ca. 0.5 mm, triangular to lanceolate, midrib thick and raised in distal 1/3, apex stoutly cuspidate; mid-series to ca. 2 mm wide, stoutly cuspidate to sometimes only slightly so; inner-series of phyllaries 10–14 × ca. 1.5

mm, lanceolate, nerves indistinct, apex narrow-acuminate but not stoutly cuspidate, membranous-scarious, neither obviously dilated nor cucullate. **Florets**: corolla 10–11.2 mm long, relatively narrowly funnelform becoming slightly salverform, white, usually glabrous throughout or lobes sometimes minutely setulose, tube 6–8 mm long, tube gradually widening into throat and together tube and throat much longer than the lobes, throat proper usually shorter than the lobes, lobes 2.5–3.2 mm long. **Cypselae** 1–1.5 mm long, densely substrigose to hirsutulous, eglandular; pappus white or dull white, outer squamellae 1–1.5 mm long, inner bristles 7–8.5 mm long, reaching to about top of involucre and to about base of corolla lobes.
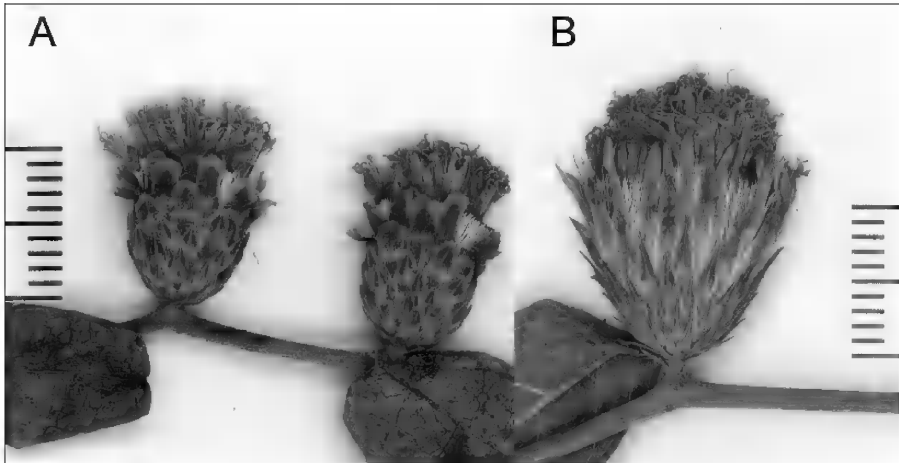
Figure 18. Involucres of (A) *Lepidaploa tortuosa* and (B) *Lepidaploa vernicosa*. In each species the pappus is held within the involucre and reaches only about to the base of the corolla lobes. A. Two capitula of *Lepidaploa tortuosa* showing the arachnoid-margined mid-series phyllaries and the obtuse to rounded apices of the mid-series and inner phyllaries. B. Capitulum of *Lepidaploa vernicosa* showing the subglabrous nitidous phyllaries, and the acute to acuminate tipped mid-series and inner-series of phyllaries. A metric scale is positioned vertically in each image. (A *Pruski et al. 4239*, MO; B *Weston 4160*, MO).

Distribution and Ecology. *Lepidaploa vernicosa* is endemic to Costa Rica, where it is occasional from 200–1100 meters elevation, and flowers mostly from December to April. The note by Standley (1938) of *L. vernicosa* being "frequent" I believe is partly in reference to plants that I would mostly determine as *L. tortuosa*. *Lepidaploa tortuosa*, however, was specifically excluded from Costa Rica by Standley.

Representative specimens. COSTA RICA. *Biolley 7013* (GH p.p., US; cited by Klatt 1892 as *V. schiedeana*); *Carvajal 115* (CR, MO); *González & González 2489* (INB, MO); *González et al. 201* (INB, MO, TEX); *Hammel et al. 18690* (INB, MO, TEX); *Hoffmann 305* (B, GH; Beaman color slide 5768; distributed from B as *V. hoffmanni* Vatke); *Khan et al. 275* (BM, MO); *Morales 6165* (INB, MO); *Pittier 16341* (US); *Scherzer s.n.* (W); *Standley 44905* (US); *Tonduz 13189* (US); *Tonduz 13607* (GH-2, NY, US; type of *V. vernicosa* var. *comosa*); *Weston 4160* (MO, UC).

By its large axillary capitula and white corollas much longer than pappus bristles, *L. vernicosa* is similar to *L. tortuosa* and was placed adjacent to it by Gleason (1906, 1922). *Lepidaploa vernicosa* (Klatt) Pruski was recognized by Standley (1938), treated in synonymy of *L. tortuosa* by Robinson (1999), and here is reinstated from synonymy. *Lepidaploa vernicosa* (Klatt) Pruski differs

from *L. tortuosa* most obviously by adaxial glabrous to strigillose (vs. strigillose or hirsute throughout or at least proximally on midrib, never glabrous) leaf blade surfaces, larger capitula, involucres glabrous or loosely arachnoid-pubescent (vs. strongly arachnoid pubescent) in bud, glabrous nitidous (vs. dull, substrigillose or subsericeous) phyllaries, the inner series of which are narrow-acuminate and neither obviously dilated nor cucullate (vs. typically constricted then dilated and cucullate and obtuse to rounded) at apex. *Lepidaploa vernicosa* is more similar to *L. tortuosa* than it is to other Central American species but these are no more similar to each other than are other the regional species pairs.

Figure 19. Fraxtiflex, large-capitulate flowering branch of *Lepidaploa vernicosa*. A metric ruler is in the lower right of the image. (*Weston 4160*, MO).

Excluded species.

Lepidaploa arborescens (L.) H. Rob., Proc. Biol. Soc. Washington 103: 481. 1990. *Conyza arborescens* L., Syst. Nat. (ed. 10) 2: 1213. 1759. *Vernonia arborescens* (L.) Sw., Fl. Ind. Occid. 3: 1320. 1806. LECTOTYPE (designated by Keeley 1982): Plumier in Burman, Pl. Amer., 122, t. 130, tab. 2, Conyza foliis ovatis. 1757. This species has been reported (e.g., Keeley 1982, 2001; Nelson 2008; Turner 2007) in Central America, with *L. canescens* in synonymy. Here, following Clewell (1975), Elias (1975), Nash (1976), and Robinson (1990, 1999), I recognize *L. canescens* (characterized in part by its usually papillose-setulose or glandular corolla tube) as distinct from *L. arborescens* (characterized in part by its glandular corolla lobe apices), the latter being interpreted as endemic to the West Indies.

Lepidaploa remotiflora (Rich.) H. Rob., Proc. Biol. Soc. Washington 103: 491. 1990. *Vernonia remotiflora* Rich., Actes Soc. Hist. Nat. Paris 1: 112 (as page "105"). 1792. LECTOTYPE (designated by Pruski 1998): **FRENCH GUIANA**. Cayenne, 1792, *LeBlond 336* (lectotype: G; isolectotypes: C, P-3, US). *Lepidaploa remotiflora* is endemic to South America, and has been

misapplied (e.g., Robinson 1990, 1999; Redonda-Martínez and Villaseñor 2011; Pruski 2013) to Central American material of *L. acilepis.* Some other Central American materials determined earlier as *L. remotiflora* are determined here variously as *L. argyropappa, L. tortuosa,* or *L. uniflora.* Similarly, *L. remotiflora* (as *Vernonia remotiflora*) was erroneously attributed by Grisebach (1863, 1866) to the West Indies but was excluded subsequently by Ekman (1914). South American *L. remotiflora* is distinguished by its gland-tipped, relatively long corolla lobes. Nevertheless, in its spinulose outer phyllaries, *L. remotiflora* is similar *L. acilepis* as well as to a larger group of species centering around *L. gracilis* (Kunth) H. Rob., each species having aristate-spinulose outer phyllary tips (Pruski 1997).

Lepidaploa salzmannii (DC.) H. Rob., *Proc. Biol. Soc. Wash.* 1032: 492. 1990. *Vernonia salzmannii* DC., Prodr. 5: 55. 1836, as "salzmanni." **TYPE: BRAZIL.** In umbrosis circa Bahiam, 1830, *Salzmann s.n.* (holotype: G-DC, as Macbride neg. 8134, as IDC microfiche 800. 774.III.4; isotype: MPU). The numbers on the sheets are taxon numbers rather than collection numbers. As mentioned in the discussion above, *L. argyropappa* is the correct name for the Mexican, Central American, and northern South American species once called *L. salzmannii* (sensu Baker 1873, non DC. 1836). *Lepidaploa salzmannii* s. str. is thus excluded from Central America and proves instead to be endemic to Brazil.

Vernonia punctata Sw. ex Wikstr., Kongl. Vetensk. Acad. Handl. 1827: 72. 1828 [in Robinson 1990, 1999 as a synonym of West Indian **Lepidaploa glabra** (Willd.) H. Rob.] was cited by Hemsley (1881: 73) as in Belize based on a Temple collection, which presumably I would determine as *L. uniflora.*

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TRES ESPECIES NUEVAS DE COMPOSITAE-ASTEREAE DE MÉXICO

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RESUMEN

Se describen e ilustran tres especies mexicanas nuevas de Compositae-Astereae, todas conocidas de una sola localidad, por lo que aparentemente representan estrechos endemismos locales. *Archibaccharis caducifolia* Rzed., **sp. nov.**, propia de la Sierra Madre del Sur de Michoacán, pertenece a la sección *Archibaccharis*, pero se distingue de los demás componentes conocidos del grupo en su porte arbustivo, hojas triplinervadas e inflorescencia en forma de panícula voluminosa. *Baccharis nesomiana* Rzed. & Zamudio, **sp. nov.**, procede del sector meridional de Tamaulipas, se ubica en la sección *Baccharis* y, en virtud de sus hojas rómbicas y dentadas, se compara con *B. halimifolia* L. así como con *B. conferta* Kunth. *Osbertia rupicola* Rzed. & Zamudio, **sp. nov.**, que se registra de la Sierra Madre Oriental de Querétaro, difiere de las tres especies previamente conocidas del género en sus involucros solo levemente graduados.

ABSTRACT

Three new Mexican species of Compositae-Astereae are described and illustrated, each of them known only from one locality and probably representing narrow local endemics. *Archibaccharis caducifolia* Rzed., **sp. nov.**, from the Sierra Madre del Sur of Michoacán, belongs to the sect. *Archibaccharis* but differs from other known members of the group in its shrubby habit, triplinervate leaves, and a large paniculate inflorescence. *Baccharis nesomiana* Rzed. & Zamudio, **sp. nov.**, from southern Tamaulipas, belongs to sect. *Baccharis* and, on account of its rhombic-dentate leaves, is compared with *B. halimifolia* L. and *B. conferta* Kunth. *Osbertia rupicola* Rzed. & Zamudio, **sp. nov.**, from the Sierra Madre Oriental of Querétaro, differs from the three previously known species of the genus in its slightly, not strongly graduate involucres.

La tribu Astereae es uno de los grandes conjuntos aparentemente monofiléticos de la familia Compositae. De sus poco más de 3000 especies conocidas, alrededor de 400 se registran de México, donde habitan mayormente áreas con pastizales, matorrales xerófilos, así como bosques de coníferas y de encinos. Son escasos sus representantes en comarcas de clima cálido húmedo y semihúmedo. Unas pocas especies son acuáticas o semiacuáticas. Varias son halófitas y/o gipsófitas. Muchas abundan en comunidades secundarias y un importante contingente se comporta como malezas.

Entre los materiales acumulados en el herbario del Centro Regional del Bajío del Instituto de Ecología, A.C. de Pátzcuaro (IEB), se encontraron algunos representantes de este grupo que corresponden aparentemente a especies sin haberse descrito todavía. Tres de ellas son objeto de este trabajo.

ARCHIBACCHARIS CADUCIFOLIA Rzed., **sp. nov.** TIPO: **MÉXICO. Michoacán.** Municipio de Coalcomán, La Yerbabuena del Naranjillo, cañada del Colorín, cañada húmeda con elementos mesófilos, alt. 1400 m, arbusto de 1.5 m de alto, escaso, 28.IV.1990, *H. Díaz B.* y *E. Pérez 6190* (IEB, isotipos por distribuirse).

Frutex erectus ca. 1.5 m altus, ut videtur dioecius vel polygamo-dioecius, per anthesin ut maximum defoliatus, glanduloso-pubescens in ramis, foliis et inflorescentiae axibus; petioli ca. 5 mm longi, laminae foliares ellipticae 3-8 cm longae, ad apicem rotundatae vel obtusae, ad basem cuneatae, ad marginem dentatae vel serratae, triplinervatae; inflorescentiae paniculiformes foliosae ad 60 cm longae et 35 cm diametro ad apicem rotundatae, pedicellis 2-4 mm longis; capitula et flores feminei ignoti; capituli masculi involucrum late campanulatum, ca. 3.5 mm altum, phyllariis 25-30 graduatis lineari-oblongis saepe ciliatis, receptaculo convexo nudo; flores per capitulum ca. 25; corolla ca. 3 mm longa glabra; styli rami appendicem linearem ca. 0.7 mm longum ferentes; pappi setae ca. 20 albae, corollam fere aequantiae, ad apicem non incrassatae.

Arbusto erecto de ca. 1.5 m de alto, aparentemente dioico o polígamodioico; ramas anguloso-estriadas, cafés, más o menos densamente cubiertas con pelos glandulosos cafés de 0.3 a 0.5 mm de largo; peciolos de ca. 5 mm de largo, láminas foliares elípticas, de 3 a 8 cm de largo, de 1.3 a 2.8 cm de ancho, redondeadas a obtusas en el ápice, cuneadas en la base, dentadas o serradas en el margen con 3 a 4 pequeños dientes por cm, triplinervadas, esparcidamente glanduloso-pubescentes en ambas superficies, de textura cartácea, al menos las principales deciduas en la época de floración; inflorescencias en forma de extensas panículas foliosas terminales hasta de 60 cm de largo y 35 cm de diámetro, redondeadas en el ápice, las hojas de la inflorescencia hasta de 2 cm de largo y 5 mm de ancho, los ejes glandular-pubescentes, pedicelos de 2 a 4 mm de largo, con frecuencia bracteolados, cabezuelas a menudo más de 200; involucro de cabezuelas masculinas anchamente campanulado, de ca. 3.5 de alto y 4 a 4.5 mm de diámetro, sus brácteas 25 a 30, graduadas en 4 series, verdes con los márgenes hialinos, todas linear-oblongas, romas en el ápice, glabras pero a menudo ciliadas al menos en la porción distal, receptáculo convexo, desnudo; flores por cabezuela ca. 25; corola tubulosa, de ca. 3 mm de largo, de color café claro, glabra, sus lóbulos de poco menos de 1 mm de largo, anteras cafés, de ca. 1 mm de largo, ramas del estilo con apéndice linear café oscuro de ca. 0.7 mm de largo, pubérulo; aquenios abortivos, vilano de ca. 20 cerdas blancas, casi del mismo largo de la corola, sin engrosamiento apical; cabezuelas y flores femeninas desconocidas.

La especie solo se registra de la localidad tipo y muy probablemente representa un endemismo de la Sierra Madre del Sur de México, misma que ha revelado muchas sorpresas para la flora de México.

Ante la falta del conocimiento de diagnósticos ejemplares femeninos, existe la posibilidad de que el taxón nuevo quede más bien ubicado en el género *Baccharis,* que agrupa plantas dioicas con mucha similitud en la morfología de cabezuelas y flores con las de *Archibaccharis*. A favor de su adscripción a este último cuentan dos características importantes:

- presencia de indumento de pelos glandulosos en tallos, hojas y ejes de la inflorescencia, carácter que no se conoce en ninguna de las numerosas especies mexicanas de *Baccharis*, pero sí se registra en varias de *Archibaccharis*;

- cerdas del vilano sin engrosamiento apical, carácter propio de *Archibaccharis*, casi sin encontrarse en flores masculinas de *Baccharis* en México.
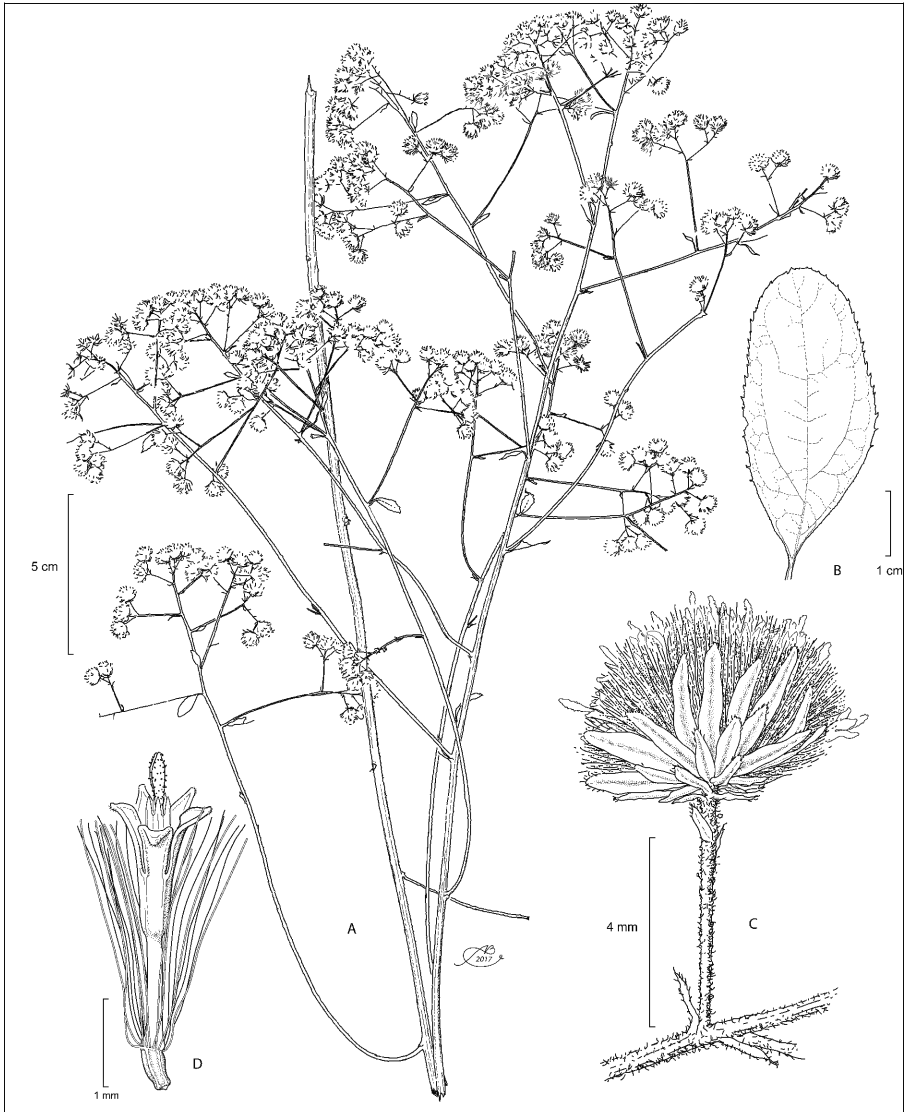
Figura 1. *Archibaccharis caducifolia*. A. Inflorescencia. B. Hoja. C. Cabezuela masculina. D. Flor masculina. Ilustrado por Alfonso Barbosa.

Dentro del conjunto de *Archibaccharis* el taxón nuevo debe ubicarse en la sección *Archibaccharis,* propuesta por Jackson (1975) y de circunscripción enmendada por Nesom (1991), pues se distingue por su cobertura de pelos glandulares y la presencia de apéndice linear en las ramas

del estilo de las flores masculinas. Sin embargo, difiere notablemente de los demás componentes del grupo en sus hojas triplinervadas, porte arbustivo, así como cabezuelas pequeñas y agrupadas en una impresionante inflorescencia en forma de extensa panícula foliosa.

El epíteto de la especie hace alusión al hecho de que la planta se encontró en pleno proceso de floración, pero prácticamente desprovista de hojas principales en abril, mes más seco del año.

BACCHARIS NESOMIANA Rzed. & Zamudio, **sp. nov.** TIPO: **MÉXICO. Tamaulipas**. Aprox. 57 km al NW de González, por la carretera a Ciudad Victoria, 21º10' N, 98º45'52'' W, laderas calizas con matorral submontano perturbado, alt. 230 m, planta arbustiva de 1.5 m, abundante, 12.XII.2003, *S. Zamudio* y *A. Ibarra 12657* (IEB, isotipos por distribuirse).

Frutex ut videtur dioecius ca. 1.5 m altus ramis ramulisque teretibus et dense puberulis; folia rhombica vel elliptica 0.8-1.5 cm longa, 2-6 mm lata, apice acuta vel acuminata, base cuneata, margine utrinque cum 2-5 dentibus prominentibus, punctata et tenua; capitula feminea plerumque solitaria et axillaria involucro turbinato 7-8 mm longo, phyllariis ca. 25 graduatis trinervatis aetate recurvatis; flores per cupitulum ca. 8; achaenia subcyllindrica ca. 3 mm longa glabra 8-10-nervata, pappus 25-30 setis laevibus ca. 5 mm longis; capitula mascula ignota.

Arbusto de ca. 1.5 m de alto, al parecer dioico, muy ramificado; ramas y ramillas teretes y densamente pubérulas con pelos por lo general crespos de ca. 0.2 mm de largo, ramillas rígidamente ascendentes en ángulos menores de 40º; hojas dispuestas densamente en las ramillas, ascendentes en forma rígida, peciolos por lo general evidentes, hasta de 3 mm de largo, láminas elípticas a más comúnmente rómbicas, de 0.8 a 1.5 cm de largo, de 2 a 6 mm de ancho, agudas a acuminadas en el ápice, cuneadas en la base, margen con 2 a 5 dientes salientes de cada lado, concentrados en los 2/3 superiores de la lámina, con un nervio central prominente y otros dos laterales partiendo de cerca de la base, de textura cartácea delgada, punteadas en ambas superficies, densamente pubérulas en la juventud, pronto glabrescentes; cabezuelas femeninas por lo común solitarias y axilares, otras veces agrupadas en especie de cortos racimos en los extremos de las ramillas, sobre pedúnculos filiformes hasta de 3 mm de largo; su involucro turbinado, de 7 a 8 mm de largo, sus brácteas ca. 25, graduadas en 4 series, de color pajizo, con 3 nervios longitudinales cafés oscuros, hialinas en el margen, agudas a acuminadas en el ápice, las interiores lineares, glabras, las más externas paulatinamente más anchas y pubérulas, con la edad todas o al menos algunas dobladas hacia fuera; receptáculo algo elevado, plano, desnudo; flores por cabezuela ca. 8, corolas filiformes, de ca. 4 mm de largo, de color café muy claro, glabras, sus lóbulos de ca. 0.5 mm de largo, ramas del estilo de color café, glabras, en la antesis sobresaliendo ca. 1 mm; aquenios casi cilíndricos, con 8 a 10 costillas longitudinales, de ca. 3 mm de largo, cafés claros, glabros, vilano de 25 a 30 cerdas blanquecinas, lisas, de ca. 5 mm de largo, dispuestas en una serie; cabezuelas y flores masculinas desconocidas.

La especie nueva solamente se conoce de la localidad tipo y muy probablemente representa un estrecho endemismo. Es notable su ubicación ecológica, pues la mayoría de los representantes mexicanos de *Baccharis* prospera en altitudes superiores a 1000 m.
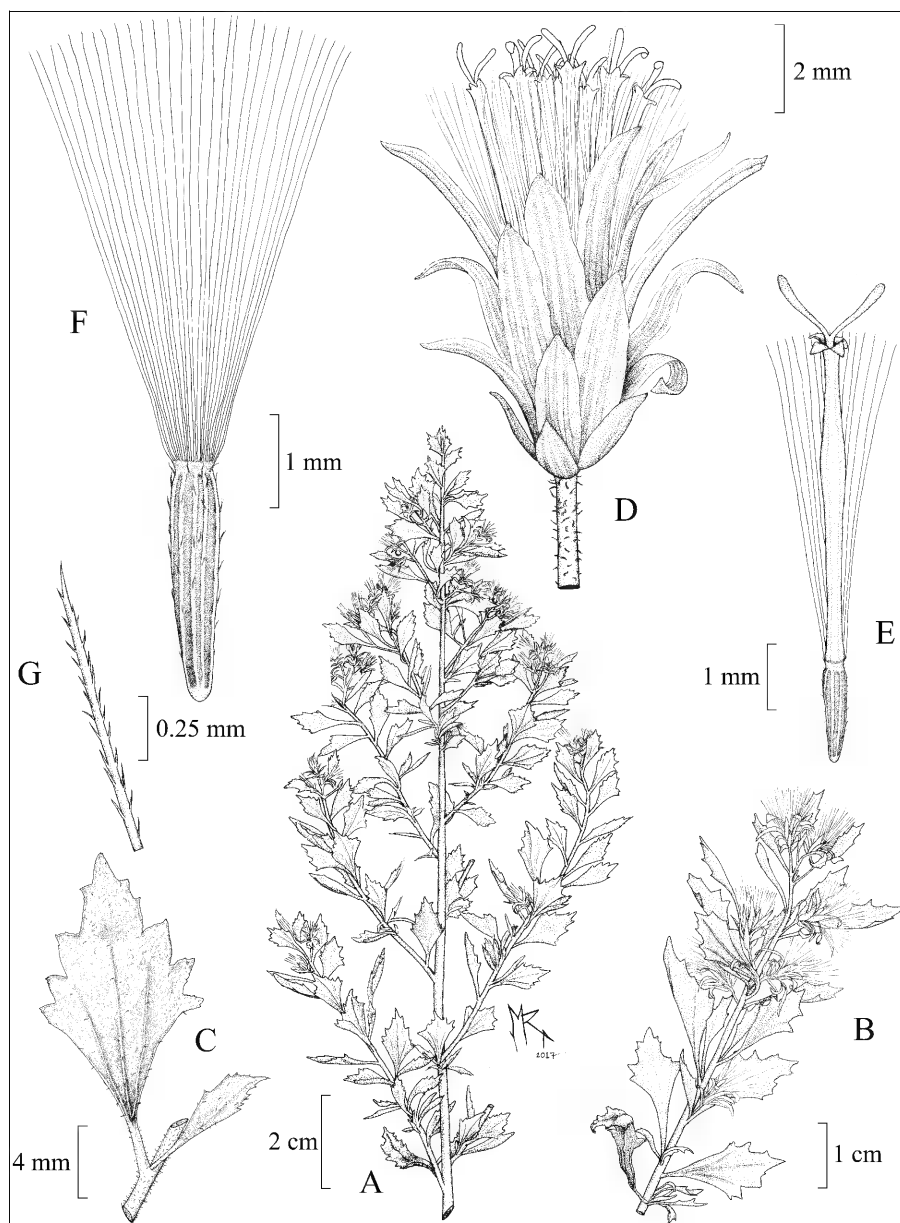
Figura 2. *Baccharis nesomiana*. A. Rama con hojas y cabezuelas. B. Rama con hojas y cabezuelas acercada. C. Hoja. D. Cabezuela femenina. E. Flor femenina. F. Aquenio. G. Segmento de una cerda del vilano. Ilustrado por José Manuel Ramírez Amezcua.

En virtud de sus hojas cuneadas en la base, trinervadas y punteadas, así como de sus aquenios glabros con 8 a 10 nervaduras, *B. nesomiana* se ubica en la sección *Baccharis* (Nesom 1990), pero no aparenta estar claramente relacionada con alguna de las especies de este grupo conocidas de Norteamérica. En sus hojas mayormente rómbicas y provistas de pocos dientes se asemeja a *B. halimifolia* L., de amplia distribución en Estados Unidos, también citada del sureste de Canadá, de las Antillas y esporádicamente registrada de México (incluyendo Tamaulipas) en calidad de halófita o gipsófita. En estos mismos caracteres *B. nesomiana* se parece a *B. conferta* Kunth, elemento frecuente de la vegetación secundaria de bosques de coníferas en el centro y sur de México, en altitudes comúnmente superiores a 1500 m. En el cuadro 1 se resumen las características diferenciales entre estas tres especies.

Caracteres	B. halimifolia	B. conferta	B. nesomiana
Ramillas			
superficie	angulosa	angulosa	terete
pubescencia	ausente	ausente	densa
Hojas			
largo en cm	3-5(7)	0.4-2	0.8-1.5
textura	gruesa	gruesa	delgada
Cabezuelas femeninas			
involucro	campanulado	campanulado	turbinado
# de flores	ca. 20	28 a 48	ca. 8
Aquenios			
largo en mm	1-1.7	1-1.5	ca. 3
Vilano			
largo en mm	(9)10-12(14)	4-6	ca. 5

Cuadro 1. Principales características diferenciales entre *Baccharis halimifolia, B. conferta, y B. nesomiana.*

El epíteto de la especie se dedica a título de reconocimiento a Guy L. Nesom, botánico norteamericano con extensa y crítica obra en el ámbito de la sistemática de fanerógamas de Estados Unidos y de México y siendo las Compositae–Astereae su grupo favorito.

OSBERTIA RUPICOLA Rzed. & Zamudio, **sp. nov**. TIPO: **MÉXICO. Querétaro**. Municipio de Landa, Llano Chiquito, 21º23'01" N, 99º06'06" W, alt. 1950 m, pastizal rodeado de bosque mesófilo de montaña, escasa sobre rocas en la orilla del arroyo, cerca del manantial, planta herbácea perenne, hojas en roseta basal, flores amarillas, 20-30.IV.2015, *S. Zamudio, D. Juárez* y *J. Hernández R. 16900* (IEB, isotipos por distribuirse).

Herba perennis scaposa estolonifera sed saepe gregaria usque 20 cm alta dense pilosa pilis ad 1.5(2) mm longis; folia principalia 18-25 rosulata oblanceolata 0.8-3.5 cm longa plerumque integra, folia caulinaria 1-3 linearia vel filiformia; caules solitarii monocephali; involucrum campanulatum vel turbinatum phyllariis leviter graduatis linearibus uninervatis longioribus 7-11 mm longis plerumque pilosis et glanduloso-pubescentibus; receptaculum leviter convexum alveolatum; flores radii 25-35 anguste lineares lutei fertiles 14-15 mm longi erecti; flores disci 40-120 tubulosi lutei ca. 7 mm longi; achaenia fere cylindrica ca. 2.2 mm longa dense pubescentia, pappus 15-20 setis 4-5 mm longis et ca. 10 setis exterioribus minus quam 1 mm longis.
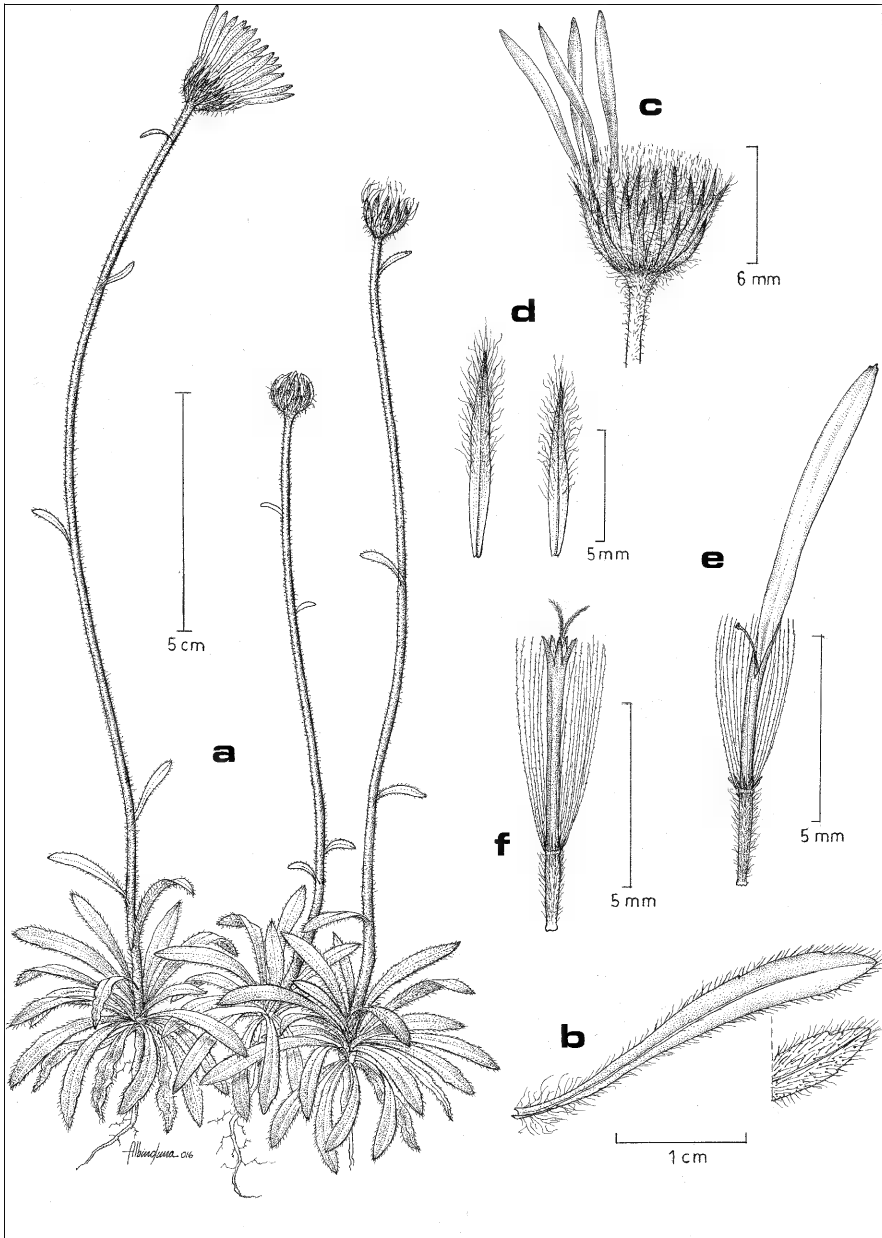
Figura 3. *Osbertia rupicola*. A. Grupo de plantas. B. Hoja. C. Cabezuela desprovista de muchas lígulas. D. Brácteas involucrales. E. Flor ligulada. F. Flor del disco. Ilustrado por Albino Luna.

Planta herbácea perenne, sin estolones pero con frecuencia tendiendo a formar agregados o masas coloniales, hasta de 20 cm de alto, densamente pilosa con pelos hasta de 1.5(2) mm de largo; hojas principales 18 a 25, dispuestas en roseta basal, oblanceoladas, de 0.8 a 3.5 cm de largo, de 1 a 4 mm de ancho, redondeadas a muy obtusas en el ápice, largamente atenuadas hacia una base pecioliforme que llega a formar casi la tercera parte de la longitud foliar, enteras o a veces inconspicuamente aserradas en el margen, hojas caulinares 1 a 3, lineares a filiformes, de 3 a 15 mm de largo; tallos escapiformes, uno por roseta, erectos, de 4 a 20 cm de largo, de 0.8 a 2 mm de diámetro; cabezuela solitaria, terminal, involucro campanulado a turbinado, sus brácteas 40 a 60, levemente graduadas, lineares, uninervadas, las más largas de 7 a 11 mm de largo, de 1 mm o poco menos de ancho, acuminadas en el ápice, las exteriores pilosas por fuera y provistas también de numerosos pelos glandulares mucho más cortos y anchos, las interiores glabras o casi glabras, receptáculo ligeramente convexo, alveolado, desnudo; flores liguladas 25 a 35, fértiles, angostamente lineares, erectas y sin enroscarse en la madurez, de 14 a 15 mm de largo, en general amarillas pero algunas con tintes rojizos en la porción distal, parte tubular pilosa, lámina glabra, de ca. 1 mm de ancho, pero casi siempre lateralmente doblada o enrollada y entonces solo de 0.4 a 0.5 mm de ancho; flores del disco 40 a 120, corola tubulosa, de ca. 7 mm de largo, amarilla, parte tubular de ca. 3 mm de largo, en general glabra pero con algunos pelos en el extremo distal, lóbulos angostamente triangulares, en general glabros pero con algunos pelos diminutos en el ápice; aquenios casi cilíndricos, algo comprimidos, de ca. 2.2 mm de largo, densamente cubiertos por pelos aplicados antrorsos, vilano de 15 a 20 cerdas cafés claras, de 4 a 5 mm de largo y con ca. 10 adicionales de menos de 1 mm de largo, ubicadas en posición externa.

Material adicional examinado. México. Querétaro. Municipio de Landa, Llano Chiquito, al E de Lagunita de San Diego, pastizal, alt. aprox. 2000 m, 1.IV.1997, *E. Carranza* y *S. Zamudio 5248* (IEB).

Osbertia rupicola solo se conoce de una localidad, donde es escasa y restringida a un hábitat especializado de rocas cercanas a un manantial. Dada esta restricción, la especie es sumamente vulnerable a la extinción.

Osbertia Greene es un pequeño grupo de Compositae - Astereae, segregado de *Haplopappus*. En su más reciente circunscripción, Nesom (2000) le adjudicó tres especies: *O. bartlettii* (S.F. Blake) Nesom, de Nuevo León y Tamaulipas, *O. chihuahuana* B.L. Turner & S. Sundberg, de Chihuahua, y *O. stolonifera* (DC.) Greene, extendida del noreste de México a Guatemala. Todas se distinguen por ser plantas herbáceas perennes rizomatosas y de porte escaposo, hojas de la roseta esencialmente oblanceoladas, tallo solitario con una sola cabezuela terminal, brácteas involucrales lineares a linear-lanceoladas, uninervadas, receptáculo convexo y alveolado, flores liguladas relativamente numerosas, muy angostas, amarillas con tintes rojizos, erectas y sin enroscarse en la madurez, así como aquenios casi cilíndricos y con muchas costillas.

Ninguno de estos caracteres es exclusivo de *Osbertia* y varios son comunes en la tribu Astereae, pero la singular combinación es la que define el grupo. *Osbertia rupicola* se ajusta bastante bien a este patrón, aunque difiere de las demás especies conocidas del género en su involucro solo escasa, no acentuadamente graduado.

A su vez, en virtud de su vilano constituido por cerdas largas internas y otras cortas externas, la especie nueva al parecer se relaciona más con *Osbertia chihuahuana*, de la cual difiere en los caracteres señalados en el Cuadro 2.

Caracteres	O. chihuahuana	O. rupicola
Estolones	presentes	ausentes
Hojas		
pubescencia	aplicada	patente
margen	entero o trífido	entero o algo aserrado
Brácteas involucrales		
disposición	imbricadas en 4 a 5 series	levemente graduadas
indumento	ciliadas en el margen, esparcidamente pubescentes con pelos glandulares cortos y anchos	las exteriores pilosas y con numerosos pelos glanulares, las interiores glabras
Flores liguladas		
largo	ca. 12 mm	14-15 mm
indumento	glabras	pilosas en la parte tubular
Cerdas largas del vilano	ca. 30, blancas	15-20, cafés claras

Cuadro 2. Características diferenciales entre *Osbertia rupicola* y *O. chihuahuana.*

La siguiente clave ayuda a separar las cuatro especies hasta ahora conocidas de *Osbertia*.

1. Plantas provistas de estolones.

    2. Cabezuelas de involucro turbinado, de 1 a 2 cm de diámetro; planta conocida de Chihuahua .... **Osbertia chihuahuana**
    2. Cabezuelas de involucro hemisférico, de 2 a 4 cm de diámetro; planta conocida del noreste de México a Guatemala .... **Osbertia stolonifera**

1. Plantas desprovistas de estolones.

    3. Tallos y hojas con pelos glandulares largos; involucro manifiestamente graduado; planta conocida conocida de Nuevo León y Tamaulipas .... **Osbertia bartlettii**
    3. Tallos y hojas desprovistos de pelos glandulares; involucro levemente graduado; planta conocida de Querétaro .... **Osbertia rupicola**

Turner y Sundberg (1986) postularon que *Osbertia* es un grupo relicto de un linaje ancestral de Astereae y su número reducido de especies unido a la distribución geográfica de las mismas están de acuerdo con tal hipótesis. Lo anterior significa que tanto *O. rupicola*, como también *O. bartlettii* y *O. chihuahuana* representan muy probablemente elementos paleoendémicos de edad considerable.

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THE GENUS *MEDICAGO* (FABACEAE) IN ALABAMA

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ABSTRACT

Seven species of *Medicago* (Fabaceae) are documented to occur in Alabama and the county distribution of each is mapped. The most common species are *M. lupulina, M. polymorpha, M. arabica,* and *M. sativa.* The less common species are *M. littoralis, M. orbicularis,* and *M. minima.* A dichotomous key and descriptions are modifications from earlier authors; all measurements, however, are based on morphological features of more than 350 specimens studied during this project. Data for the county-level distribution maps were compiled entirely from herbarium vouchers.

The genus *Medicago* was established in *Species Plantarum* (Linnaeus 1753). The name is derived from the Greek "Media," which is a land east of Greece and thought to be the area where alfalfa (*M. sativa* L.) originated. The common name "medic" or "medick" is derived from the same source (Wilbur 1963). The genus consists of 83 species of shrubs and herbs, which have a geographical distribution from the Mediterranean region to central Asia (Lackey 1981). Of these, 19 taxa have been introduced to the USA (Kartesz 2015), 7 species in the southeastern USA (Isely 1990), and 6 species in Alabama (Kral et al. 2011).

Medicago is a member of the legume family Fabaceae (Leguminosae), subfamily Papilionoideae, tribe Trifoliae, subtribe Trigonellinae (Small 1989). The evolutionary history of *Medicago* remains unresolved because of conflicting published gene phylogenies (de Sousa 2014). However, six of these gene phylogenies were compared and hybridization was found between several of the taxa within *Medicago.* Therefore, the phylogenetic history of the genus is better understood in the context of complex reticulate evolution instead of a standard dichotomous tree" (de Sousa et al. 2016).

The primary objectives of this study were to determine which species of *Medicago* occur in Alabama and report county-level distribution for each. Additional goals included providing a dichotomous key, species descriptions, and photographs.

Materials and methods

Data for the distribution maps were gathered from personal collections and more than 350 plant specimens deposited in the herbaria of Troy University (TROY), Anniston Museum of Natural History (AMAL), Botanical Research Institute of Texas (BRIT), John D. Freeman Herbarium at Auburn University (AUA), Jacksonville State University (JSU), Samford University (SAMF), University of Alabama (UNA), University of North Alabama (UNAF), University of South Alabama (USAM), and University of West Alabama (UWAL).

The dichotomous key is a modification of Wilbur (1963), Isely (1990), and Weakley (2015); however, all measurements are based on morphological features of the vegetative and reproductive structures of the plants examined during this project. Descriptions for each taxon are based on those of Isely (1990) and Afonin et al. (2008), with modifications incorporating measurements taken from the specimens studied. The lists of specimens examined are limited to one record from each county.

Herbarium specimens were initially divided into groups based on overall morphological similarity and the species concept established by Isely (1990) and Weakley (2015). Morphological measurements were made from selected specimens of each group. Field studies were also conducted to observe the species in their natural habitats and make personal collections

Results

Based on the results of this study, the dispersion of *Medicago* species in the state is represented by these figures: *M. lupulina* (41 counties), *M. polymorpha* (21 counties), *M. arabica* (16 counties), *M. sativa* (11 counties), *M. orbicularis* (7 counties), *M. littoralis* (2 counties), and *M. minima* (1 county).

TAXONOMIC TREATMENT OF *MEDICAGO* IN ALABAMA

Medicago L., Sp. Pl. 778. 1753, nom. cons.

Annual or perennial herbs or low shrubs. **Stems** prostrate, ascending, decumbent or erect, 0.3–8 dm, glabrous, strigose, pilose or villous. **Leaflets** elliptical to obovate or obcordate, 0.2–3 cm long, 0.2–3.2 cm wide, apically dentate or notched, lanate or villous beneath; stipules entire or dentate to lacerate or laciniate. **Inflorescence** racemes, ovoid to capitate or oblong, 1–25 flowers. **Calyces** 1–6 mm long; corolla 2–6 mm long, yellow, glabrous, pilose, lanate or villous. **Fruits** reniform or coiled 2–6 turns, 2–2.5 mm wide, 1.5–2 mm long, spiny or spineless, tan, brown or black at maturity, glabrous or pubescent. **Seeds** 1 to several.

KEY TO THE ALABAMA SPECIES OF *MEDICAGO*

1. Fruits 1-seeded, reniform, black at maturity; corolla 2–3 mm long .... **Medicago lupulina**
1. Fruits several seeded, spirally coiled, tan or dark brown; corolla 3–11 mm long.

  2. Plants perennial, ascending to erect (-prostrate), 2–8 (–10) dm tall; corolla 6–11 mm long, violet, yellow, or varicolored; fruits spineless .... **Medicago sativa**
  2. Plants annual, prostrate or ascending, 1–6 dm tall; corolla 3–6 mm long, yellow; fruits spiny (lacking spines in *M. orbicularis*).

    3. Stipules entire or slightly dentate; stems villous .... **Medicago minima**
    3. Stipules lacerate or laciniate; stems glabrous or strigose.

      4. Fruits spineless; stipules deeply lacerate, the sinuses extending nearly to the base
      .... **Medicago orbicularis**
      4. Fruits spiny; stipules shallowly or deeply lacerate or laciniate.

        5. Leaflets appressed lanate below; calyces 4–6 mm, appressed lanate ... **Medicago littoralis**
        5. Leaflets glabrous beneath; calyces 2–3.5 mm long, glabrous or strigose.

          6. Stipules not divided beyond the middle, teeth 0.5–2 mm long; leaflets 0.7–1.1 times as long as wide, usually with a central dark spot, apex strongly notched .... **Medicago arabica**
          6. Stipules divided beyond the middle, teeth 2–6 mm long; leaflets 1–2 times as long as wide, central dark spot absent, apex shallowly notched .... **Medicago polymorpha**

1. **Medicago lupulina** L., Sp. Pl. 779. 1753.
   Medica lupulina (L.) Scop. Fl. Carniol., ed. 2. 2: 88. 1772.
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Medicago willdenowii Boenn., Prodr. Fl. Monast. Westphal. 226. 1824, non Merat. 1812

Medicago lupulina var. *corymbosa* Ser., in de Candolle, Prodr. 2:172. 1825.

Medicago lupulina var. *polystachya* Ser., in de Candolle, Prodr. 2: 172. 1825.

Medicago lupulina var. *unguiculata* Ser., in de Candolle, Prodr. 2: 172. 1825.

Medicago corymbifera Schmidt ex Schltdl., Linnaea 4: 74. 1829

Medicago lupulina var. *vulgaris* Koch, Syn. Fl. Germ. Helv. 161. 1835, nom. inadmiss.

Medicago lupulina var. *willdenowiana* Koch, Syn. Fl. Germ. Helv. 161. 1835.

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Medicago cupaniana Guss., Fl. Sicul. Syn. 2: 362. 1844.

Lupularia parviflora Opiz, Seznam 61. 1852, nom. illegit.

Medicago lupulina var. *willdenowii* Asch., Fl. Brandenburg 1: 139. 1867, nom. illegit.

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Medicago lupulina var. *stipularis* (Wallr.) Hallier, in W. D. J. Koch, Syn. Fl. Germ. Helv., ed. 3. 534. 1891.

Medicago lupulina var. *perennans* Grossh., Fl. Kavk. 2: 260. 1930.

Annual herb. **Stems** prostrate or ascending, 4-angled, 0.5–8 dm, glabrous to pilose. **Leaflets** broadly to narrowly cuneate-obovate, 0.8–1.5 cm long, 0.25–0.75 cm wide, apically denticulate, villous or sparsely pubescent beneath; stipules entire or toothed. **Inflorescence** racemes, ovoid, 10–25 ascending flowers. **Calyces** 1.5 mm long; corolla 2–3 mm long, yellow, glabrous. **Fruits** reniform-incurved, 1.5–2 mm wide, spineless, black at maturity, glabrous (-pubescent). **Seeds** 1. Figure 1.

Specimens examined. Baldwin Co.: 23 Mar 2006, *Diamond 16183* (TROY). Bibb Co.: 1 Apr 1999, *Brodeur, Whetstone & Hobson 1631* (JSU). Bullock Co.: 31 Jan 2013, *Dykes 1487* (TROY). Butler Co.: 7 Jan 2007, *Diamond 17276* (TROY). Calhoun Co.: 4 Mar 1992, *Clearman & Spaulding 31* (JSU). Chilton Co.: 10 Apr 2005, *Diamond 15079* (BRIT). Coffee Co.: 10 Apr 2000, *Martin 543* (TROY). Colbert Co.: 26 Jun 2014, *England 5000* (TROY). Conecuh Co.: 24 Mar 1986, *Diamond 2208* (AUA). Coosa Co.: 30 May 2013, *Diamond 24145* (TROY). Covington Co.: 25 Mar 2005, *Diamond 15032* (TROY). Crenshaw Co.: 30 Apr 2000, *Diamond 11677* (TROY). Cullman Co.: 20 Apr 1975, *Whetstone 4785* (JSU). Dale Co.: 15 May 1993, *Austinhirst 45* (TROY). Dallas Co.: 9 May 1966, *Basms s.n.* (AUA). Etowah Co.: 27 May 1994, *Hodge & Spaulding 1332* (JSU). Fayette Co.: 6 Apr 2002, *Spaulding 11161* (TROY). Franklin Co.: 17 May 1968, *Kral 30581* (BRIT). Geneva Co.: 25 Jan 2007, *Diamond 17285* (TROY). Greene Co.: 5 Jun 1968, *Kral 31080* (BRIT). Houston Co.: 13 Dec 2013, *Diamond 24704* (TROY). Jackson Co.: 27 Jun 1998, *Brodeur, Whetstone, & Hoffman 938* (JSU). Jefferson Co.: 2 Apr 1976, *Whetstone, Atkinson & Hinton 7995* (JSU). Lamar Co.: 6 Apr 2002, *Spaulding 11174* (TROY). Lawrence Co.: 19 Jan 2000, *England 101* (UNA). Lee Co.: 20 Apr 1969, *Burton 153* (AUA). Limestone Co.: 26 May 1996, *Spaulding 8938* (AMNH). Macon Co.: 24 Apr 2006, *Diamond 16281* (TROY). Madison Co.: 11 May 1996, *Spaulding & Threlkeld 8343* (JSU). Marengo Co.: 4 Jun 2010, *England 2481* (UWAL). Marshall Co.: 3 Apr 1992, *Spaulding 1265* (JSU). Mobile Co.: 4 Mar 2007, *Keener 3338* (TROY). Montgomery Co.: 21 Dec 2005, *Diamond 16090* (TROY). Morgan Co.: 4 Apr 1969, *Nee & Peet 1631* (BRIT). Pike Co.: 19 Mar 1997, *Evers 15* (TROY). Randolph Co.: 12 Aug 1972, *Pounders 189* (AUA). Shelby Co.: 29 Apr 1978, *Harding 8119* (UNA). Sumter Co.: 10 Jul 2006, *Keener & England 3184* (TROY). Talladega Co.: 1 Mar 2008, *Keener 4036* (TROY). Tallapoosa Co.: 17 Mar

2002, *Spaulding 11117* (TROY). <u>Tuscaloosa Co.</u>: 4 Apr 1981 *Meigs & Horn 200* (UNA). <u>Walker Co.</u>: 17 Apr 1982, *Whetstone & Whetstone 9489* (UWAL). <u>Wilcox Co.</u>: 20 May 1982, *Gunn 650* (AUA).

Native of Europe. Habitat and distribution in Alabama: clay soils of roadsides, railroad right-of-ways, vacant lots; throughout Alabama.

2. **Medicago sativa** L., Sp. Pl. 778. 1753.
   Medica sativa (L.) Lam., Fl. Franc. 2: 584. 1779 ("1778").
   Medica legitima Greene, Man. Bot. San Francisco 101. 1894, nom. illegit
   Medicago pauciflora Ledeb., Fl. Ross. 1: 526. 1843.
   Medicago sativa var. *pilifera* Urb., Verh. Bot. Vereins Prov. Brandenburg 15: 57. 1873.
   Medicago sativa subsp. *macrocarpa* Urb., Verh. Bot. Vereins Prov. Brandenburg 15: 57. 1873, nom. inadmiss.
   Medicago sativa var. *falcata* Urb., Verh. Bot. Vereins Prov. Brandenburg 15: 57. 1873, non. inadmiss.
   Medicago sativa var. *grandiflora* Grossh., Obs. Dr.-Kavk. Medicago 28. 1919.
   Medicago sativa var. *parviflora* Grossh., Obs. Kr.-Kavk. Medicago 28. 1919.
   Medicago agropyretorum Vassilcz., Bot. Zurn. SSSR 26 (1): 32. 1941.
   Medicago caerulea var. *pauciflora* (Ledeb.) Grossh., in Komarov, Fl. URSS 11: 151. 1945.
   Medicago grandiflora (Grossh.) Vassilcz., Vol. Sci. Works Leningrad 1941-1943: 101. 1946.
   Medicago mesoptamica Vassilcz., Bot. Zurn. SSSR 31 (3): 27. 1946.
   Medicago rivularis Vassilcz., Vol. Sci. Works Leningrad 1941-1943: 101. 1946.
   Medicago sogdiana Vassilcz., Vol. Sci. Works Leningrad 1941-1943: 101. 1946.
   Medicago transonxana Vassilcz., Vol. Sci. Works Leningrad 1941-1943: 101. 1946.
   Medicago caucasica Vassilcz., Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk. SSSR 13: 141. 1950.
   Medicago lavrenkoi Vassilcz., Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk SSSR 13: 141. 1950.
   Medicago praesativa Sinskaya, Kulturnaja Fl. SSSR 13(1): 51. 1950.
   Medicago asiatica Sinskaya, Fl. Cult. Pl. USSR 13: 70. 1951.
   Medicago karatschaica Latschaschv., Not. Syst. Geogr. Inst. Bot. Tibilissi 21: 29. 1959.

Perennial herb. **Stems** prostrate or ascending, 2–8 dm, glabrous to villous. **Leaflets** obovate to oblong-oblanceolate, 1–2.5 cm long, 0.2–1.7 cm wide, apically denticulate, villous beneath; stipules entire or proximally dentate. **Inflorescence** racemes, ovoid to oblong, 8–25 ascending flowers. **Calyces** 4–5.5 mm long; corolla 2–3 mm long, purple or varicolored 8–11 mm long, glabrous or villous. **Fruits** coiled 2–3 turns, 4–6 mm wide, spineless, tan at maturity, glabrous or pubescent. **Seeds** several. Figure 2.

Specimens examined. <u>Baldwin Co.</u>: 14 May 1983, *Wilhelm 11329* (BRIT). <u>Cherokee Co.</u>: 5 May 1994, *Ballard & Ballard 7303* (BRIT). <u>Covington Co.</u>: 22 Dec 2007, *Diamond 18692* (TROY). <u>Cullman Co.</u>: 1 Aug 1903*, Wolf 877* (AUA). <u>Dekalb Co.</u>: 26 Jul 1975, *Wayner & Wayner 549* (JSU). <u>Etowah Co.</u>: 7 May 1995, *Hodge & Spaulding 4241* (JSU). <u>Jackson Co.</u>: 26 May 1999, *Brodeur, Whetstone & Spaulding 1847* (JSU). <u>Lee Co.</u>: 15 May 1922, *Simmons s.n.* (TROY). <u>Montgomery Co.</u>: 12 May 1963, *Elkins s.n.* (AUA). <u>Pike Co.</u>: 4 Feb 2013, *Diamond 23720* (TROY). <u>St. Clair Co.</u>: 13 Jul 1969, *Day s.n.* (TROY).

Native of Europe and west Asia. Habitat and distribution in Alabama: dry, sandy roadsides, railroad right-of-ways, pastures; northeast, east-central and south Alabama.

3. **Medicago minima** (L.) Bartal., Cat. Piante Siena 61. 1776.
   Medicago polymorpha var. *hirsuta* L., Sp. Pl. 780. 1753.
   Medicago polymorpha var. *minima* L., Sp. Pl. 780. 1753.
   Medicago hirsuta Bartal., Cat. Piante Siena 61. 1776.
   Medicago mollissima Roth, Catal. Bot. 3:74. 1806.
   Medicago graeca Hornem., Hort. Bot. Hafn. 728. 1815.
   Medicago minima var. *longiseta* DC. ex Ser., in de Candolle, Prodr. 2: 178. 1825.
   Medicago lineata Tausch, Flora 14: 210. 1831.
   Medicago minima var. *brevispina* Benth., in Smith, Engl. Bot. Suppl. 1: t. 2635. 1831.
   Medicago minima var. *brachydon* Bartal., Fl. Germ. Excurs. 502. 1832.
   Medicago minima var. *brachydon* Bartal., var. *brachyodon* Reichenb., Fl. Germ. Excurs. 502.
      1832.
   Medicago minima var. *mollissima* (Roth) Koch, Syn. Fl. Germ. Helv. 164. 1835.
   Medicago minima var. *viscida* Koch, Syn. Fl. Germ. Helv. 164. 1835.
   Spirocarpus minimus (L.) Opiz, Seznam 93. 1852.
   Medicago pulchella Lowe. Trans. Cambridge Philos. Soc. 6 (reimpt.): 25. 1858.
   Medicago minima var. *pulchella* (Lowe) Lowe, Man. Fl. Madeira 1: 166. 1862.
   Medicago meyeri Gruner, Bull. Soc. Imp. Naturalistes Moscou 40(2): 416. 1867.
   Medicago brachyacantha Kerner, Oesterr. Bot. Z. 18: 386. 1868.
   Medicago minima forma *mollissma* (Roth) Urb., Verh. Bot. Vereins Prov. Brandenburg 15: 79.
      1873.
   Medicago minima var. *vulgaris* Urb., Verh. Bot. Vereins Prov. Brandenburg 15: 78. 1873, nom.
      inadmiss.
   Medicago minima forma *viscida* (Koch) Urb., Verh. Bot. Vereuns Prov. Brandenburg 15: 78.
      1873.
   Medicago sessilis Peyr. ex Post, Fl. Syria 10. 1896.
   Medica hirsuta Bubani, Fl. Pyren. 2: 477. 1899.
   Medicago inconspicua Navski, Trudy Bot. Inst. Akad. Nauk SSSR, Ser. 1 Fl. Sist. Vyss. Rast. 4:
      250. 1937.
   Medicago minima subsp. *brevispina* Ponert, Feddes Repert. 83: 639. 1973 ("1972"), nom.
      inadmiss.

   Annual herb. **Stems** procumbent or ascending, 1–4 dm, villous. **Leaflets** obovate-cuneate to elliptic 0.4–1.2 cm long, 0.2–1.0 cm wide, toothed toward apex, notched, lanate beneath; stipules entire or slightly dentate. **Inflorescence** racemes, subcapitate, 3–6 flowers. **Calyces** 2–2.5 mm long; corolla 3–5 mm long, yellow, lanate. **Fruits** commonly clustered, 3–5 per peduncle, coiled 3–4 turns, 6–8 mm wide, spiny, tan at maturity, pubesecent. **Seeds** several. Figure 3.

   Specimens examined. Mobile Co.: 4 Apr 2010, *Barger & Holt 256* (AMNH).

   Native of Mediterranean region. Habitat and distribution in Alabama: disturbed areas, ballast soils; Mobile County.

4. **Medicago orbicularis** (L.) Bart., Cat. Piante Siena 60. 1776.
   Medicago polymorpha var. *orbicularis* L. 1753.
   Medicago polymorpha var. *orbicularis* L., Sp. Pl. 779. 1753.
   Medicago inermis Lam., Fl. Franc. 2: 586. 1779
   Medica orbicularis Medik., Vorles. Churpfaelz. Phys.-Oecon. Ges. 2:386. 1787.
   Medicago marginata Willd., Enum. Pl. 2:802. 1809.
   Medicago orbicularis var. *microcarpa* Rouy, Fl. France 5: 18. 1899, non Seringe 1825.
   Medicago orbicularis var. *marginata* (Willd.) Benth., Cat. Pl. Pyrenees 100. 1826.
   Medicago cuneata Woods, Tourist's Fl. 84. 1850.

Annual herb. **Stems** prostrate, sometimes mat forming, 1–4 dm, glabrous. **Leaflets** cuneate-obovate, 0.7–1.5 cm long, 0.4–1.5 cm wide, apically dentate, glabrous beneath; stipules deeply lacerate, sinuses extending more than halfway or nearly to base, glabrous to strigose. **Inflorescence** racemes, subcapitate, 1–2 loosely spaced flowers. **Calyces** 2.5–3 mm long; corolla 3–5 mm long, yellow, ephemeral, strigose. **Fruits** coiled 3–5 turns, 1–1.5 mm wide, spineless, tan at maturity, glabrous. **Seeds** several. Figure 4.

Specimens examined. Calhoun Co.: 1 Jun 1998, *Tucker s.n.* (JSU). Franklin Co.: 25 May 1970, *Kral 39114* (BRIT). Jackson Co.: 26 May 1999, *Brodeur, Whetstone & Spaulding 1875* (JSU). Lee Co.: 19 Jul 1966, *Rogers s.n.* (AUA). Marshall Co.: 28 Apr 1998, *Spaulding 10507* (JSU). Mobile Co.: 1 Aug 1892, *Mohr s.n.* (UNA). Morgan Co.: 13 May 2011, *England 2875* (UWAL).

Native of Mediterranean Eurasia and North Africa. Habitat and distribution in Alabama: dry, sandy roadsides, railroad right-of-ways, limestone glades; north Alabama, east-central Alabama and extreme southwest Alabama.

5. **Medicago littoralis** Rohde ex Loisel., Not. Pl. Fl. France 118. 1810.
  Medicago truncatula subsp. *littoralis:* Rohde ex Loisel., Feddes Repert. 83: 639. 1973.

Annual herb. **Stems** prostrate or ascending, multiple branching from base, cylindrical, 0.3–3 dm, glabrous toward base, pubescent upper part. **Leaflets** obtrullate to widely obovate, 0.2–0.9 cm long, 0.4–1.1 cm wide, dentate to serrate, apically notched, appressed lanate beneath, stipules laciniate. **Inflorescence** racemes ovoid, 1–6 ascending flowers. **Calyces** 4–6 mm long; corolla 4–6 mm long, yellow, appressed lanate. **Fruits** coiled 2–6 turns, 2–6 mm wide, spiny, tan at maturity, glabrous. **Seeds** several. Figure 5.

Specimens examined. Baldwin Co.: 26 Mar 2014, *Spaulding 13900* (UWAL). Mobile Co.: 14 May 2013, *Horne 2176* (UWAL).

Native of Mediterranean coasts. Habitat and distribution in Alabama: disturbed dunes, sand patches; extreme southwest Alabama.

6. **Medicago arabica** (L.) Huds., Fl. Angl. 288. 1762.
  Medicago polymorpha var. *arabica:* L., Sp. Pl. 708. 1753
  Medica echinata: Lam., Fl. Franc. 2: 587. 1779 ("1778"), nom. illegit.
  Medica arabica: (L.) Medik., Vorles. Churpfaelz. Phys.-Oecon. Ges. 2: 386. 1787.
  Medicago cordata: Desvaux., in Lam., Encycl. 3: 636. 1792, nom. illegit.
  Medicago maculata: Sibth., Fl. Oxon. 232. 1794, nom. illegit.
  Medicago arabica subsp. *inermis* (L.) Huds. subsp. *inermis* Ricker, U.S.D.A. Bur. Pl. Industr.
    Bull. 267: 33. 1913.

Annual herb. **Stems** decumbent to erect, 0.3–5 dm, glabrous or pilose. **Leaflets** cuneate-obovate or obcordate, denticulate or undulate-margined, 0.8–3 cm long, 0.8–3.2 cm wide, emarginated, usually medially maculate, glabrous or with some persistent pubescence below most with a dark spot, stipules shallowly lacerate, sinuses extending less than half of their length, glabrous or occasionally appressed villous beneath. **Inflorescence** racemes, subcapitate, 2–4 contiguous flowers. **Calyces** 2–2.5 mm long; corolla 4–5 mm long, yellow, glabrous. **Fruits** coiled 4–6 turns, 9–14 mm wide, spiny, tan at maturity, glabrous. **Seeds** several. Figure 6.

Specimens examined. Bullock Co.: 22 Feb 2012, *Dykes 305* (TROY). Calhoun Co.: 6 Apr 1968, *O'Neal s.n.* (TROY). Colbert Co.: 30 Apr 1944, *Isely 3180* (BRIT). Conecuh Co.: 17 Mar

1986, *Diamond 2108* (AUA). Coosa Co.: 24 Apr 1972, *Lochamy 95* (AUA). Dallas Co.: 21 Mar 1972, *Kral 45363* (BRIT). Hale Co.: 23 Apr 1996, *Williams 226* (UNA). Houston Co.: 29 Mar 1991, *MacDonald 1243* (BRIT). Jefferson Co.: 11 Apr 2013, *Davenport 5426* (SAMF). Lee Co.: 17 Mar 2002, *Spaulding 11113* (TROY). Macon Co.: 9 Apr 1967, *Raukin 55* (AUA). Marengo Co.: 12 Apr 2009, *England 1946* (TROY). Mobile Co.: 27 Mar 1965, *Deramus 310* (UNA). Montgomery Co.: 16 Mar 1977, *Harvey 91* (UNA). Pike Co.: 1 Apr 1989, *Blanton s.n.* (TROY). Sumter Co.: 10 Apr 2010, *Keener 5759* (UWAL). Tuscaloosa Co.: 12 Apr 1959, *Edwards s.n.* (UNA).

Native of Mediterranean region. Habitat and distribution in Alabama: sandy soil in vacant lots, railroad right-of-ways; throughout Alabama.

7. Medicago polymorpha L., Sp. Pl. 779. 1753.

Medicago polymorpha var. *ciliaris* (Seringe) Shinners, Rhodora 58: 9. 1956, non L. 1753.
Medicago polymorpha var. *nigra* L., Mant. Pl. 454. 1771.
Medica polymorpha (L.) Scopoli, Fl. Carnoli., Ed. 2. 2: 89. 1772
Medicago nigra (L.) Krock., Fl. Siles. 2(2): 244. 1790.
Medicago hispida Gaertn., Fruct. Sem. Pl. 2: 349. 1791, nom. illegit.
Medicago lappacea Desr, in Lamarck, Encycl. 3: 637. 1792, nom. illegit.
Medicago apiculata Willd., Sp. Pl. 3: 1414. 1802.
Medicago pentacycla DC., Cat. Pl. Horti Monsp. 124. 1813.
Medicago denticulata var. *ciliaris* Seringe, in de Candolle, Prodr. 2: 176. 1825.
Medicago reticulata Benth., Cat. Pl. Pyrenees 101. 1826.
Medicago denticulata var. *brevispina* Benth., Cat. Pl. Pyrenees 103. 1826.
Medicago denticulata var. *lappacea* Benth., Cat. Pl. Pyrenees 103. 1826, nom. illegit.
Medicago pentacycla var. *vulgaris* Benth., Cat. Pl. Pyrenees 104. 1826. nom. inadmiss.
Medicago denticulata var. *vulgaris* Benth., Cat. Pl. Pyrenees 103. 1826. nom. inadmiss.
Medicago sardoa Moris ex G. Don, Gen. Hist. 2: 170. 1832
Medicago apiculata var. *confinis* Koch, Syn. Fl. Germ. Helv. 164. 1835.
Medicago denticulata var. *macracantha* Webb & Berth., Hist. Nat. Iles Canaries 3(2(2)): 64.
    1842.
Medicago lappacea var. *pentacycla* (DC.) Godr., Fl. France 1: 390. 1849.
Medicago lappacea var. *tricycla* Godron, in Gren. & Godr., Fl. France 1: 390. 1849, nom. illegit.
Medicago polycarpa var. *tuberculate* Godr., in Gren. & Godr., Fl. France 1: 390. 1849, nom.
    illegit.
Medicago polymorpha var. *tricycla* (Godr.) Shinners, Rhodora 58: 8. 1856.
Medicago lappacea var. *macracantha* (Webb & Berth.) Lowe, Man. Fl. Maderia 1: 158. 1862.
Medicago hispida forma *tuberculata* Urb., App. Observe. Bot. 4. 1873.
Medicago hispida forma *apiculata* Urb., App. Observe. Bot. 4. 1873.
Medicago hispida forma *inermis* Urb., App. Observe. Bot. 4. 1873.
Medicago hispida var. *oligogyra* Urb., App. Observ. Bot. 4. 1873.
Medicago hispida var. *pentacycla* (DC.) Urb., Verh. Bot. Vereins Prov. Brandenburg 15: 75.
    1873.
Medicago hispida var. *polygyra* Urb., App. Observ. Bot. 4. 1873.
Medicago hispida var. *tricycla* (Godr.) Urb., App. Observ. Bot. 3. 1873.
Medica apiculata (Willd.) Greene, Man. Bot. San Francisco 102. 1894.
Medica denticulata (Willd.) Greene, Man. Bot. San Francisco 102. 1894
Medicago hispida var. *apiculata* (Willd.) Burnat, Fl. Aples Marit. 2: 106. 1896.
Medicago hispida var. *confinis* (Koch) Burnat, Fl. Apes Marit. 2: 106. 1896
Medica reticulata (Benth.) Bubani, Fl. Pyren. 2: 480. 1899.
Medicago hispida forma *sardoa* (Moris ex G. Don) Asch. & Graebn., Syn. Mitteleur. Fl. 6(2):
    433. 1907.

Medicago hispida var. *reticulata* (Benth.) Asch. & Graebn., Syn. Mitteleur. Fl. 6(2): 431. 1907.
Medicago polymorpha forma *apiculata* (Willd.) Shinners, Rhodora 58: 11. 1956.
Medicago polymorpha forma *tuberculata* (Urb.) Shinners, Rhodora 58: 11. 1956.
Medicago polymorpha var. *polygyra* (Urb.) Shinners, Rhodora 58: 9. 1956.
Medicago polymorpha var. *vulgaris* (Benth.) Shinners, Rhodora 58: 310. 1956.
Medicago polymorpha var. *brevispina* (Benth.) Heyn., Scripta Hierosolymitana 12: 77. 1963.

Annual herb. **Stems** prostrate or ascending, commonly mat forming, 0.5–5 dm, glabrous.
Leaflets cuneate-obovate to obcordate, 0.8–2 cm long, 0.6–2 cm wide, apically dentate, emarginated,
not maculate, glabrous or appressed villous beneath, medial and upper stipules deeply lacerate,
sinuses usually more than halfway. **Inflorescence** racemes, subcapitate, 2–5 contiguous flowers.
Calyces 3–3.5 mm long; corolla 3.5–6 mm long, yellow, glabrous. **Fruits** coiled 2–6 turns, 7–12 mm
wide, spiny, brown to black at maturity, glabrous. **Seeds** several. Figure 7.

Specimens examined. Baldwin Co.: 4 Mar 2007, *Keener 3342* (TROY). Barbour Co.: 16
Mar 2002, *Spaulding 11103* (TROY). Butler Co.: 4 Mar 2007, *Diamond 17296* (TROY). Chilton
Co.: 15 Apr 2007, *Spaulding 12578* (TROY). Choctaw Co.: 24 Apr 1994, *Crouch 897* (BRIT).
Coffee Co.: 3 May 2000, *Martin 673* (TROY). Conecuh Co.: 10 Mar 2009, *Diamond 20508*
(TROY). Covington Co.: 10 Mar 2008, *Diamond 18744* (TROY). Crenshaw Co.: *Diamond 12379,*
22 Apr 2001 (TROY). Dale Co.: *Rundell 689,* 23 Feb 1999 (TROY). Geneva Co.: 6 Mar 2008,
Diamond 18735 (TROY). Greene Co.: 6 May 1967, *Naugle 279* (UNA). Henry Co.: 13 Jan 2013,
Diamond 23647 (UWAL). Houston Co.: 13 Dec 2013, *Diamond 24703* (TROY). Lee Co.: 28 Mar
1964, *Bozarth s.n.* (JSU). Macon Co.: 29 Mar 2012, *Barger 488* (AUA). Marengo Co.: 20 Apr 2013,
England, England & Keener 4141 (UWAL). Mobile Co.: 11 Apr 1980, *Lelong 11047* (USAM).
Montgomery Co.: 8 Feb 2009, *Diamond 20492* (TROY). Morgan Co.: 1 Apr 1883, *Mohr 303*
(UNA). Pike Co.: 23 Mar 1989, *Rutledge s.n.* (TROY). Sumter Co.: 18 May 1973, *Kral 50132*
(BRIT).

Native of Mediterranean region and southern Europe. Habitat and distribution in Alabama:
sandy and clay soils in vacant lots, roadside, railroad right-of-ways; southern one-half of Alabama.

DISCUSSION
In Alabama, plants of *Medicago* grow in sandy and clay soils of vacant lots, roadsides,
railroad right-of-ways, and pastures. All seven taxa of *Medicago* in the state are introduced from
Europe, West Asia, and the Mediterranean region. None of these taxa is considered invasive.

A combination of reproductive and morphological characteristics is used to differentiate the
species of *Medicago* in Alabama. *Medicago lupulina* is the most easily recognized taxon with one-
seeded, reniform fruits. The remaining taxa have spirally coiled fruits with several seeds. *Medicago
arabica* is also easily recognized by a central dark spot on most of the leaflet. Both *M. sativa* and *M.
orbicularis* have spineless fruits, whereas, the remaining three taxa have fruits with spines. *Medicago
sativa* and *M. orbicularis* are distinguished from one another by their inflorescence. The
inflorescence of *M. sativa* has between 8–25 flowers, whereas, *M. orbicularis* inflorescence has 1–2
loosely spaced flowers. Of the remaining three taxa, *M. minima* is recognized by entire or slightly
dentate stipules and villous stems. The stipules of *M. littoralis* and *M. polymorpha* are lacerate or
laciniate and the stems are glabrous or strigose. *Medicago polymorpha* has leaflets 0.8–2 cm long
and calyces 3.0–3.5 mm long, whereas, *M. littoralis* has leaflets 0.2–0.9 mm long and calyces 4–6
mm long.
In the most recent checklist of the vascular plants of Alabama, six species of *Medicago* were
reported (Kral et al. 2011). The seventh species reported in this treatment, *M. littoralis*, is based on
collections from Baldwin and Mobile Counties in March of 2013. Small (1933) reported *Trigonella*

monspeliaca L. (*Medicago monspeliaca* (L.) Trautv. from dry soils, fields and hillsides in the coastal plain of Alabama, but he did not give a specific locality. The report of this taxon occurring in Alabama on the USDA, NRCS website (2017) is likely based on the report by Small (1933). Kartesz (2015) reported *M. monspeliaca* as introduced into the northeastern USA and the closest location to Alabama is Maryland. Since no vouchers of this taxon were found and attempts to locate it in the field were unsuccessful, it is excluded from this study and is considered extirpated from the state, or else the previous report was based on misidentified material.

Medicago sativa (alfalfa) is the most economically important species in the genus. It is considered one of the world's primary crop plants with an annual value as high as a trillion dollars (Small 2011). In the USA, it is one of the most widely grown crops for pasture, or for hay, silage, or green chop. Although it has been grown in the southeastern USA since the late 19th century, it has not attainted the status that it has in other parts of the nation (Lacefield et al. 2009). In Alabama, *M. sativa* has been cultivated in the Black Belt and the northern part of the state but seldom in south Alabama (Harper 1944). One of the main reasons for its lack of cultivation in south Alabama is that frequent rainfall and high humidity are not conducive to harvesting alfalfa as hay (Ball 2017).
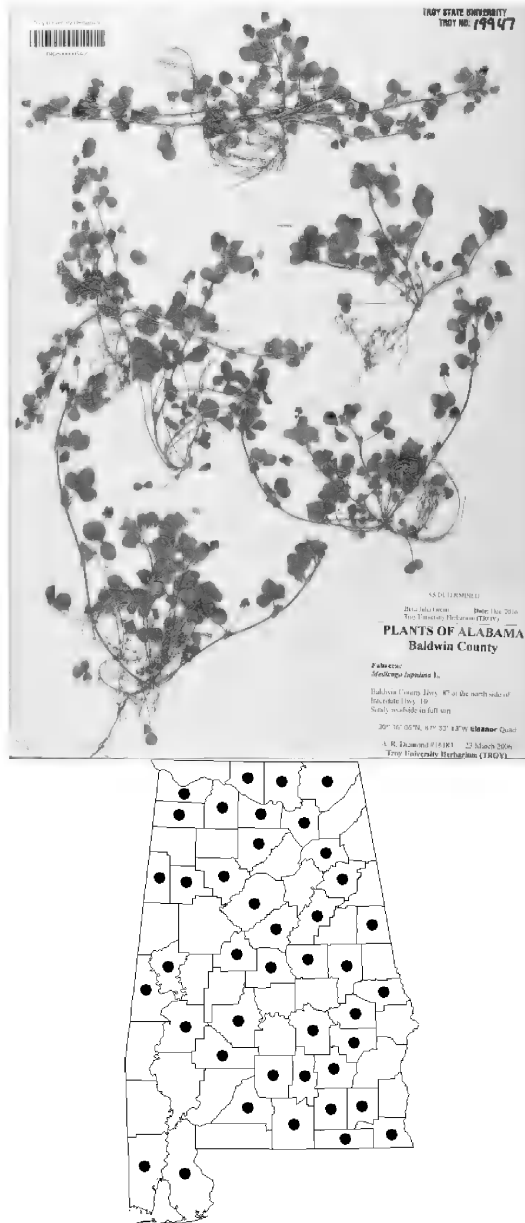
Figure 1. *Medicago lupulina*, distribution.

Figure 2. *Medicago sativa*, distribution.

Figure 3. *Medicago minima*, distribution.
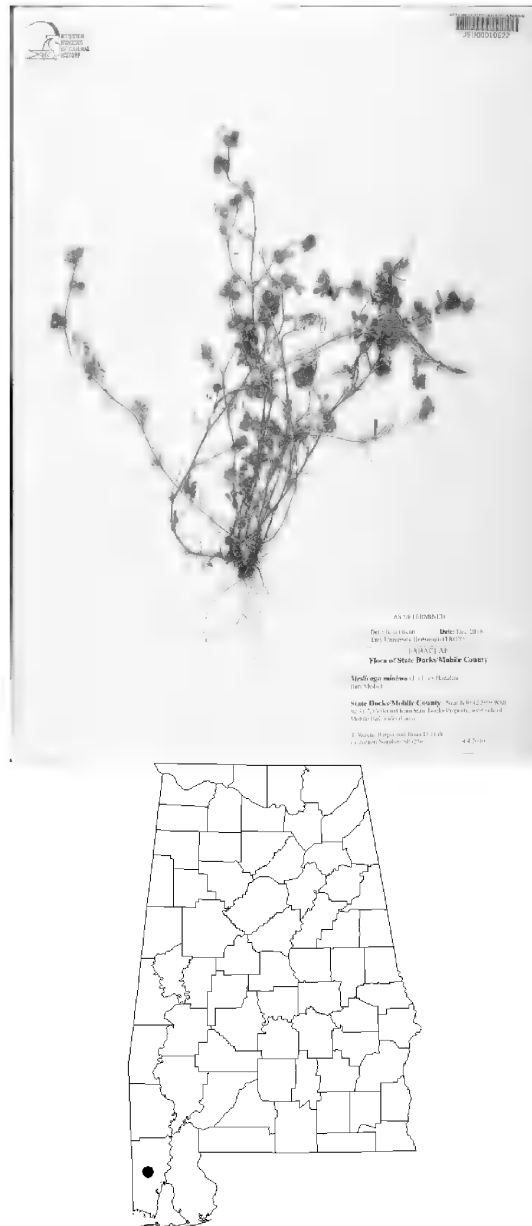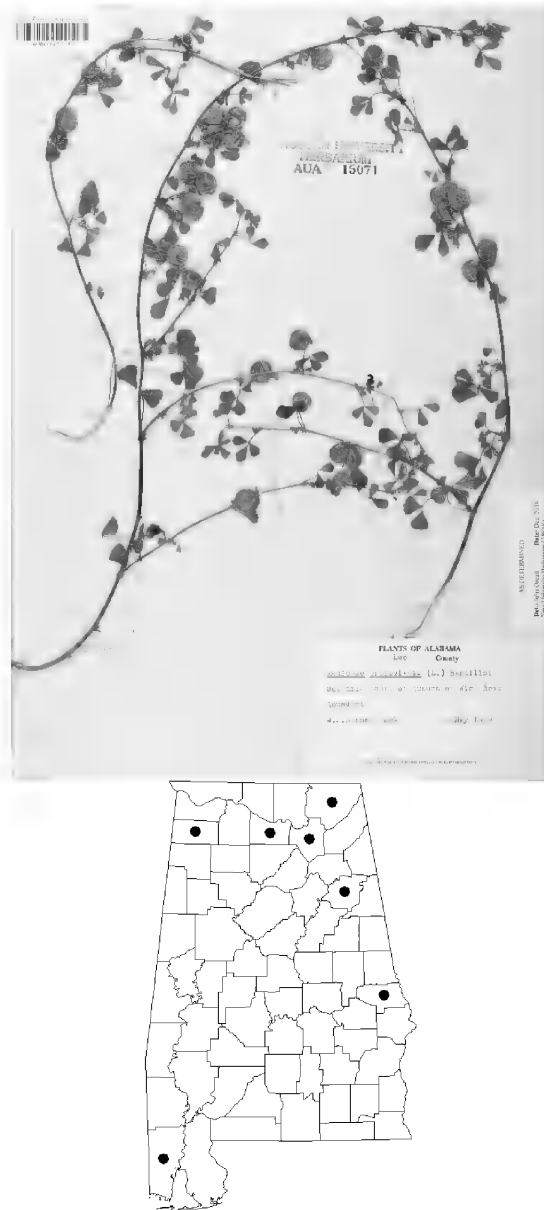
Figure 4. *Medicago orbicularia*, distribution.

Figure 5. *Medicago littoralis*, distribution
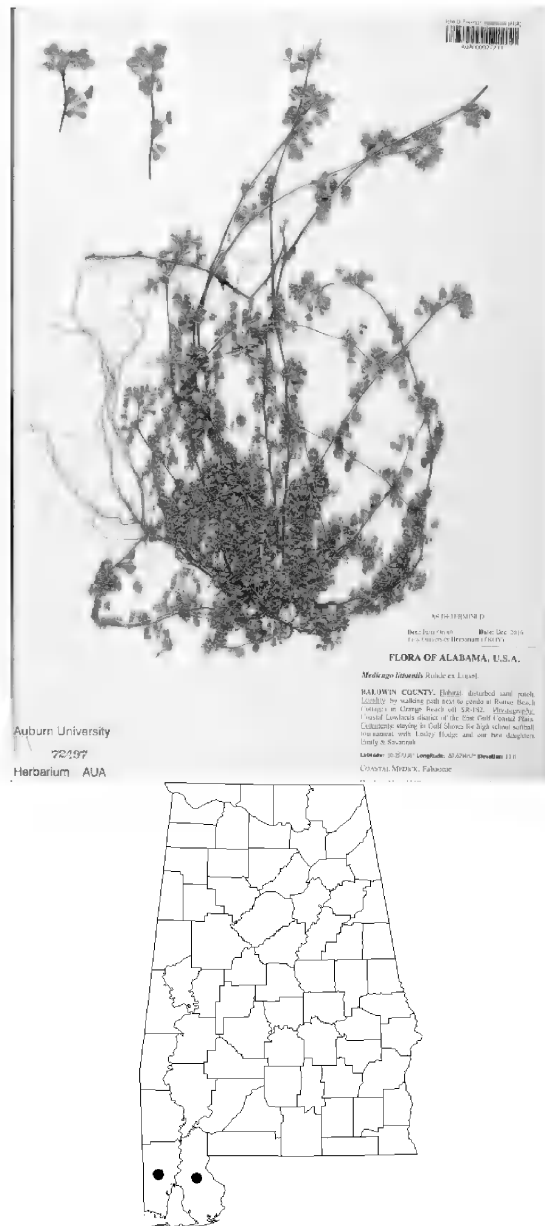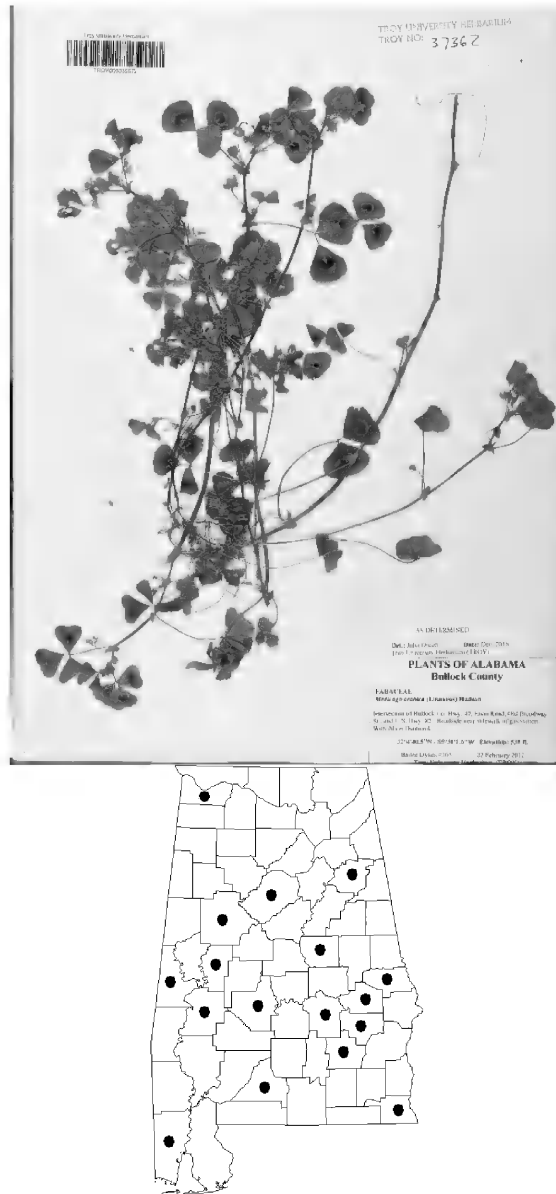
Figure 6. *Medicago arabica*, distribution
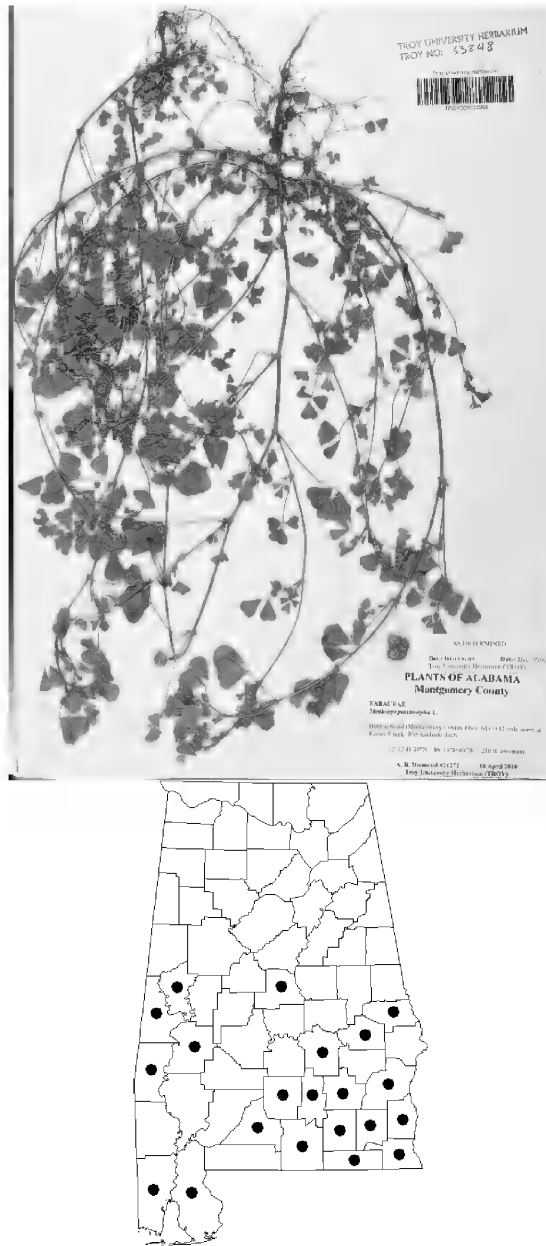
Figure 7. *Medicago polymorpha*, distribution.

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CARICA PAPAYA (CARICACEAE) AS A PROBABLE WAIF IN CENTRAL TEXAS

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ABSTRACT

Recent collection of *Carica papaya* in Lee County confirms the presence of mature specimens of the species in central Texas. The species at this location is considered to be a waif mostly likely established from discarded fruit spread by animals. This non-cold tolerant species perhaps has persisted at the location because of warmer than average temperatures during the past two winters. It is not expected to become naturalized.

We report *Carica papaya* (Caricaceae), the papaya tree, collected in a natural habitat about 450 km north of areas where it is cultivated in extreme south Texas (Holmes 2010), based on the specimen cited below.

TEXAS: Lee Co.: private ranch 8.85 km SW of Giddings, Texas, near community of Serbin, along the edges of game trails in post oak woodland openings, in fruit, 8 Nov 2016, *Dickschat 1* (BAYLU). Figures 1, 2, and 3.

Two populations of *Carica papaya* were documented on private ranchland in Lee County. The first location included one reproductively mature tree, with a cluster of immature trees and three seedling trees sprouting in close proximity. The second population included a reproductively mature specimen (ca. 13 cm diameter and 2.3 m tall) with several seedling trees. Both populations were found in woodland openings dominated by *Chasmanthium latifolium*, *Smilax bona-nox*, *Callicarpa americana*, *Croton capitatus*, *Ilex vomitoria*, *Juniperus virginiana*, and *Quercus stellata*.

Carica papaya (Caricaceae), the papaya tree, or *lechoso*, is a softwood tree cultivated worldwide for its fruits, leaves, and flowers as a food, vitamin, and mineral source (Holmes 2010). It has also been recognized as having a role in a wide range of medical and surgical conditions in traditional medicine (Morton 1978; Duke 1985), including burn treatment (Starleya et al. 1999).

Liquid papaya extract has been used for treatment of warts, corns, and cancers, the roots for piles and yaws, the leaves for nervous pains and the fruit for infected wounds, malignant tumors and blistering (Morton 1978). Papaya has also been used in industrial and other pharmaceutical applications including various cosmetic and textiles as well as ornamental landscaping (Holmes 2010).

Carica papaya is found in various tropical regions, e.g., Central and South America and west Africa (Holmes 2010). Cultivated for centuries, it has been found naturalized in Florida from the southern Keys north to Collier County (West & Arnold 1946; Wunderlin 1998; Ward 2011).

Based on distribution maps of papaya in tropical regions and in areas of pantropical introductions, including south Texas, a mature central Texas specimen is surprising based on climatic conditions. Likely establishment of this specimen occurred by mammalian or bird vectors (see description in Mink et al. 2015) similar to fruiting exotics established and previously documented in the state; e.g., *Carissa macrocarpa* (Singhurst & Holmes 2010), *Jasminum laurifolium* (Mink et al. 2015), *Asparagus aethiopicus* (Singhurst et al. 2016), and *Cupaniopsis anacardioides* (Mink et al. 2017).

Lethal low temperature for *Carica papaya* is -0.9 C (Whiteman 1957) and plants are able to withstand brief periods of frost (Snyder & Paulo de Melo-Abreu 2005). Climatic data sets (PRISM 2017) recorded no temperatures beyond the published critical low for *C. papaya* for Serbin, Texas, from 8 March 2015 until time of collection, 8 November 2016 (20 months). Plants are dioecious or gynodioecious (Teixeira da Silva et al 2007) and thus require another individual for fertilization. Given the prolific, short-lived, and fast-growing life history of *C. papaya* (Holmes 2010), fruits can be expected 10 to 14 months after germination (Teixeira da Silva et al 2007).

Figure 1. *Carica papaya* in understory forest of Lee Co., Texas. Photo by Jason R. Singhurst, 13 October 2016.

Permanent establishment of *Carica. papaya* in the Texas flora seems unlikely based on frost-sensitivity of the plant and historical mean temperatures of central Texas. Litz (1984) listed latitudes between 32' N and S as a delimiting growth zone. However, under particular cycles of unseasonably warm weather, periodic waifs, including reproductively mature specimens, could be encountered.

Figure 2. *Carica papaya* specimen (*T. Dickschat 1*) prior to mounting, Lee Co., Texas. Photo by Jason R. Singhurst, 8 November 2016.
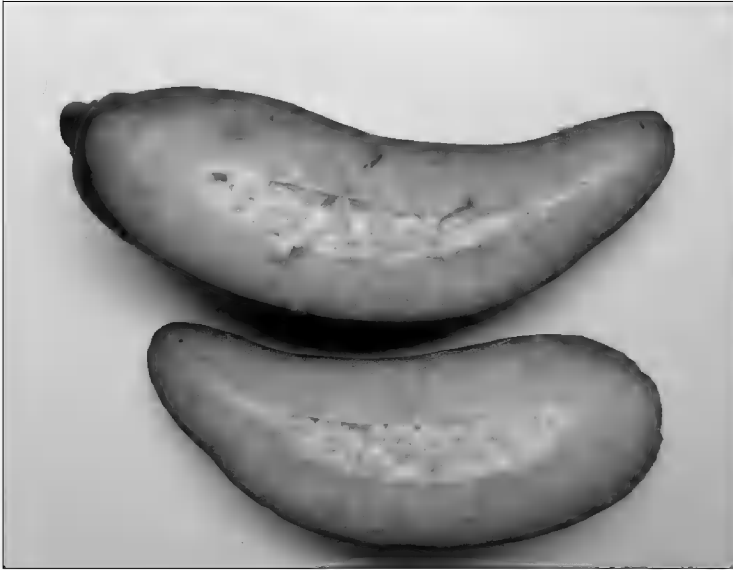
Figure 3. *Carica papaya* fruit specimen (*T. Dickschat 1*) prior to pressing, Lee Co., Texas. Photo by Jason R. Singhurst, 8 November 2016.

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SOLIDAGO GEORGIANA (ASTERACEAE: ASTEREAE), A NEW SPECIES IN *S.* SUBSECT. *SQUARROSAE* FROM GEORGIA

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ABSTRACT

Solidago georgiana is described from a single collection from Effingham Co., Georgia. The new species is placed in *Solidago* subsect. *Squarrosae* and has morphological similarities with *S. roanensis* and *S. porteri.*

Solidago subsect. *Squarrosae* A. Gray (Asteraceae: Astereae) includes 14 species native primarily to eastern Canada and the midwestern and eastern portions of the USA (Semple et al. 2017). Semple and Cook (2006) recognized 9 species with multiple infraspecific taxa in several species, while Semple (2017 frequently updated) recognized 14 species: *S. bicolor* L., *S. erecta* Pursh, *S. hispida* Muhl., *S. jejunifolia* Steele, *S. pallida* (Porter) Rydb., *S. porteri* Small, *S. puberula* Nutt., *S. pulverulenta* Nutt., *S. rigidiuscula* (Torr. & A. Gray) Porter, *S. roanensis* Porter, *S. sciaphila* Steele, *S. speciosa* Nutt., *S. squarrosa* Muhl., and *S. villosicarpa* LeBlond. A total of 265 specimens representing 14 species were included in a multivariate study of *S.* subsect. *Squarrosae* focusing on the *S. speciosa* complex (Semple et al. 2017).

As part of an in-progress multivariate study of the *Solidago puberula - S.pulverulenta* complex, additional collections were borrowed from GA (Thiers continuously updated) to expand the sampling of the complex in Georgia. Among the collections was *Zomlefer et al. 3785* from Effingham County near the coast in southeastern Georgia, northwest of Savannah, which had been identified originally as *S. puberula* then later annotated as *S. puberula* subsp. *pulverulenta* (Nutt). Semple. The stem pubescence was not densely very-short canescent from the base into the inflorescence and the heads appeared to be too big and the phyllaries too wide for *S. puberula* and *S. pulverulenta*. Hairs were absent from the lower stem and became increasingly more dense distally and were longer than hairs found on stems of *S. puberula* and *S. pulverulenta* and more like the pubescence of *S. roanensis* in distribution and size as noted in the multivariate study of the *S. bicolor-S. hispida* complex (Figs. 5-6 in Semple et al. 2017). However, the range of *S. roanensis* just extends into northern Georgia in the Appalachian Mountains with the nearest known collections coming from Abbeville Co., South Carolina, in the Piedmont at 150-200 m elevation (Fig. 13 in Semple et al. 2017). *Zomlefer et al. 3785* came from the outer coastal plain at about 19 m elevation (Figs. 1-2).

The involucres of *Solidago roanensis* are 2.3–5.6 mm tall, averaging 3.9 mm tall (Table 15 in Semple et al. 2017). The involucres of *Zomlefer et al. 3785* average about 5 mm tall. Ray lamina lengths in *S. roanensis* are 1–3 mm averaging about 2 mm while those of *Zomlefer et al. 3785* were about 4 mm long. Thus, the heads of *Zomlefer et al. 3785* are noticeably larger and more showy than those of *S. roanensis*. Either *Zomlefer et al. 3785* is a significantly disjunct and possibly polyploid member of *S. roanensis* with only diploids $2n=18$ having been reported for the species (Beaudry 1963, Semple et al. 1984, Semple et al. 2015 and unpublished data), or it is a collection of a previously undescribed species. Because the habitats of *Zomlefer et al. 3785* and *S. roanensis* are so different, treating the former as a member of a previously undescribed species is the more reasonable option in this case. Semple et al. (2017) included *Zomlefer et al. 3785* in a multivariate study of *S. porteri*, *S. roanensis*, *S. squarrosa*, and *S. villosicarpa*; *Zomlefer et al. 3785* was most similar to *S. porteri* but also had affinities to *S. roanensis* and *S. villosicarpa*.

Figure 1. Holotype of *Solidago georgiana*, *Zomlefer et al. 3785* (GA from Effingham Co., Georgia.
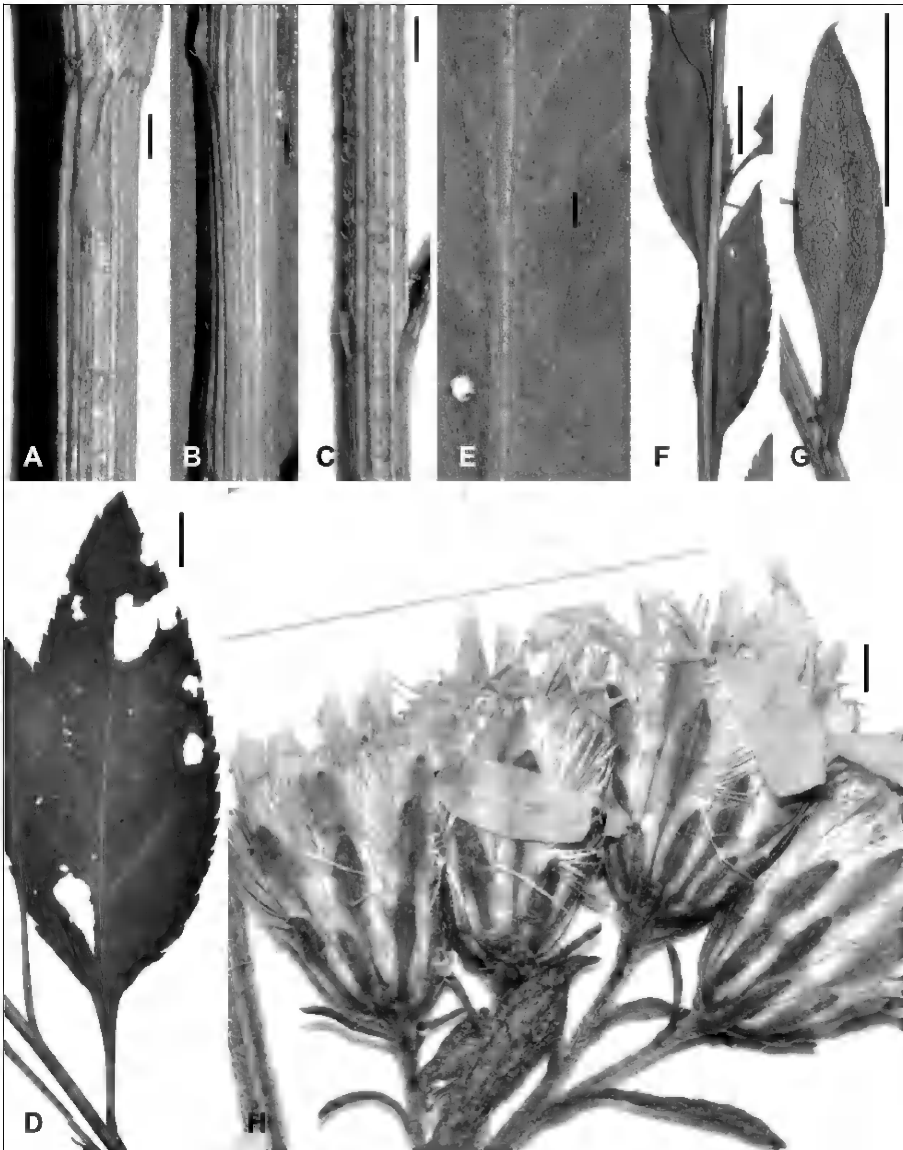
Figure 2. Details of the morphology of the holotype of *Solidago georgiana, Zomlefer et al. 3785* (GA). **A-C.** Lower, middle and upper stem. **D-E.** Lower stem leaf and adaxial surface detail. **F-G.** Mid and upper stem leaves. **H.** Heads. Scale bars = 1 mm in A-C, E and H; = 1 cm in D, F-G.

SOLIDAGO GEORGIANA Semple, **sp. nov**.   TYPE: USA. **Georgia**: Effingham Co.: Guyton, 925 Riverside Drive [property owned by Craig Barrow], ca. 1012 ha (2500 acres) bordered by the Ogeechee River and Riverside Drive, along dirt road through clear-cut area (sandhill with planted pine); *Eupatorium* spp. and *Pitochaetium avenaceum*, plants scattered in open area along road, just beginning to flower, infrequent (sporadic), lat. 32.3429° N, long. 81.4722° W, 8 Sep 2014, *W.B. Zomlefer 3785 with C. Barrow, D.E. Giannasi, & S. Hughes* (holotype: GA). Figures 1 and 2)

Similar to *Solidago roanensis* in stem pubescence but with larger more showy heads that are smaller than those of *Solidago porteri* and native to the outer coastal plain of southeastern Georgia.

Plants 65–75 cm; from short rhizomes. **Stems** single, erecta, glabrous proximally, strigulose-puberulent distally and in arrays. **Leaves:** basal and proximal cauline tapering to narrowly winged petioles 20–35 mm long, blades elliptic to elliptic-ovate, 70–110 (including petiole) × 20–38 mm newly formed rosettes with much smaller leaves, acuminate, glabrous, margins serrate and scabrellous; mid and distal cauline sessile, blades mostly narrowly lanceolate, 18–50 × 4–12 mm. **Heads** 20–50, in elongate, narrowly paniculiform arrays, leafy-bracteate proximally, not secund, proximal branches short and ascending to arching. **Peduncles** 3–10 mm, bracteolate. **Involucres** campanulate, 5-5.1 mm at anthesis. **Phyllaries** in 3–4 series, appressed, unequal (outer $^1/3$ length of inner), linear to lanceolate-deltate, single veined, apices broadly acute to slightly obtuse. **Ray florets** 4–6; laminae 3.9–4.5 × 1.4–1.7 mm. **Disc florets** 8–10; corollas 4.3–4.8 mm, lobes 0.7–1.1 mm. Cypselae: body 1.1-1.3 mm at anthesis, proximally sparsely strigose, distally moderately densely strigose; pappus in several similar series, the longest inner 3.5-3.8 mm at anthesis; mature fruits larger. **Chromosome number**: unknown.

The species is currently known only from the holotype collection.

ACKNOWLEDGEMENTS

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MULTIVARIATE STUDIES OF *SOLIDAGO* SUBSECT. *SQUARROSAE*. III. *S. GEORGIANA, S. PORTERI, S. ROANENSIS, S. SQUARROSA,* AND *S. VILLOSICARPA* (ASTERACEAE: ASTEREAE)

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ABSTRACT

Solidago subsect. *Squarrosae* includes a number of larger-headed, often showy species that are native to eastern North America. *Solidago squarrosa* is widely distributed in eastern Canada south to the mountains in North Carolina, while *S. georgiana, S. porteri* and *S. villosicarpa* are narrowly distributed rare endemics in the southeastern USA. All five species have hairless lower stems and variously hairy mid and upper stems. A multivariate analysis of these four species and the smaller-headed *S. roanensis* was performed to compare and contrast the species.

Solidago subsect. *Squarrosae* A. Gray (Asteraceae: Astereae) includes more than a dozen species native primarily to eastern Canada and the midwestern and eastern portions of the USA (Semple et al. 2017). Semple and Cook (2006) recognized 9 species with multiple infraspecific taxa in several species, while Semple (2017, 2017 frequently updated) recognized 15 species: *S. bicolor* L., *S. erecta* Pursh, *S. georgiana* Semple, *S. hispida* Muhl., *S. jejunifolia* Steele, *S. pallida* (Porter) Rydb., *S. porteri* Small, *S. puberula* Nutt., *S. pulverulenta* Nutt., *S. rigidiuscula* (Torr. & A. Gray) Porter, *S. roanensis* Porter, *S. sciaphila* Steele, *S. speciosa* Nutt., *S. squarrosa* Muhl., and *S. villosicarpa* LeBlond.

All species of subsect. *Squarrosae* except *S. georgiana* were included in a multivariate study focusing on the *S. speciosa* complex (Semple et al. 2017). *Solidago porteri* (Figs. 1-2), *S. squarrosa* (Figs. 3-5) and *S. villosicarpa* (Figs. 6-8) were most strongly separated in that study and had larger heads than other species; *S. roanensis* was more centrally located in the plot of canonical scores and had smaller heads (see Figs. 5-6 and 13 in Semple et al. 2017). *Solidago georgiana* was described from a single collection by Semple (2017) in the companion paper to this study. *Solidago georgiana* has intermediate sized heads and stems that lack hairs proximally but become increasingly more hairy from mid stem to upper stem into the inflorescence (Figs 1-2 in Semple 2017), while stem hair distribution is similar in *S. porteri, S. roanensis, S. squarrosa* and *S. villosicarpa*; hair size varies within and between these five species.

Solidago roanensis, S. squarrosa, and *S. villosicarpa* have been reported to be diploid $2n=18$ (Beaudry & Chabot 1959; Beaudry 1963; Beaudry 1969; Kapoor 1970; Kapoor 1977; Semple et al. 1981; Semple et al. 1984; Semple & Chmielewski 1987; Semple & Cook 2004; Semple et al. 2015; unpublished data). *Solidago porteri* was reported to be hexaploid $2n=54$ (Semple & Estes 2015). The chromosome number of *S. georgiana* is unknown; Semple (2017) speculated that it might be a polyploid due to involucre size or a larger-headed diploid like *S. squarrosa* and *S. villosicarpa*.

Results of a multivariate analysis of *Solidago georgiana, S. porteri, S. squarrosa* and *S. villosicarpa* are reported here. *Solidago georgiana* (1 population in Georgia), *S. porteri* (5 populations in Tennessee, Alabama, and Georgia) and *S. villosicarpa* (3-4 populations in North Carolina) are narrowly distributed rare endemics in the southeastern USA (Fig. 9), while *S. squarrosa* is widely distributed in eastern Canada south to the mountains in North Carolina (Fig. 10).

Figure 1. Morphology of *Solidago porteri* (*Semple et al. 11861*, unmounted) from Giles Co., Tennessee.
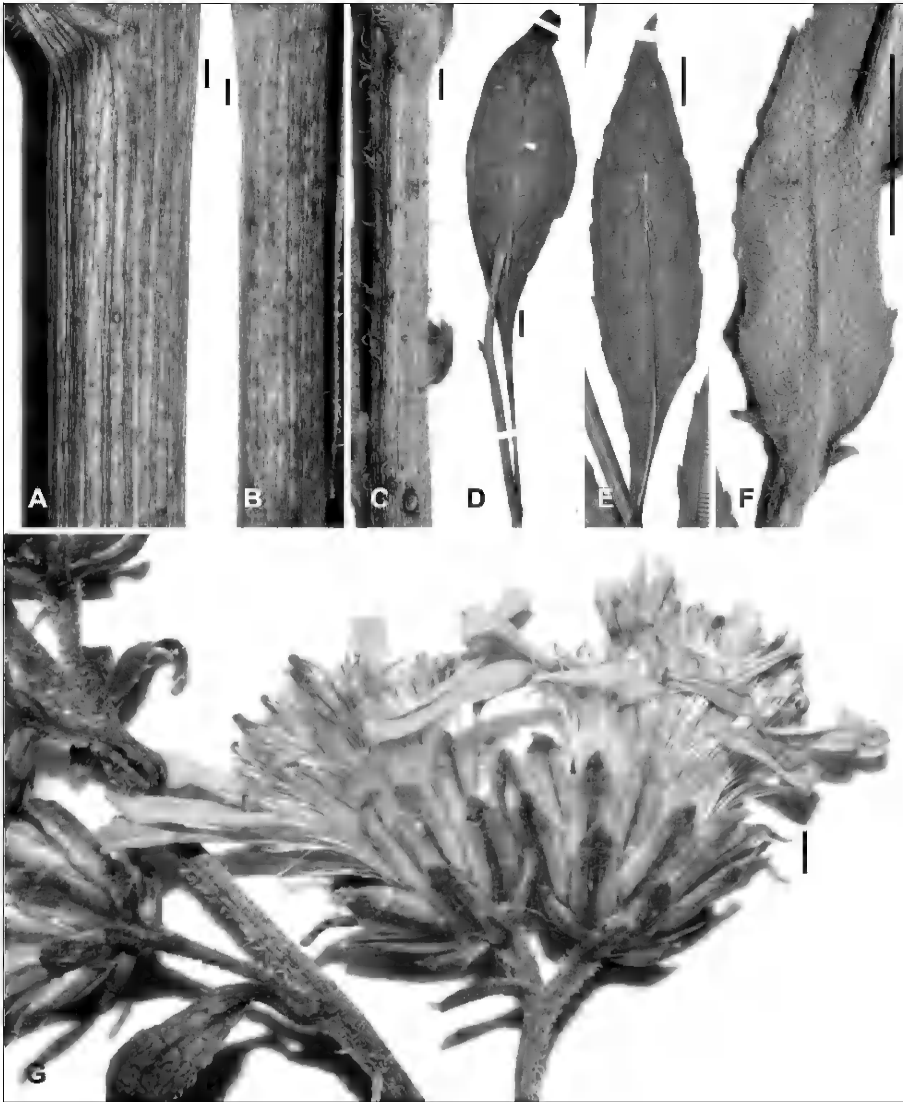
Figure 2. Details of the morphology of *Solidago porteri*. **A-C.** Lower, lower middle and upper stems. **A.** *Patrick et al 22001* (GA); robust shoot. **B-C.** *Semple & B. Semple 11190* (WAT). **D.** Lower stem leaf, adaxial surface, *Hill 1162b-1* (GA). **E.** Mid stem leaf, *Hill 1162a* (GA). **F.** Upper stem leaf, abaxial surface, *Semple & B. Semple 11190* (WAT). **G.** Heads, *Hill 1162c-6* (GA).   Scale bars = 1 mm in A-C, and G; = 1 cm in D-F.
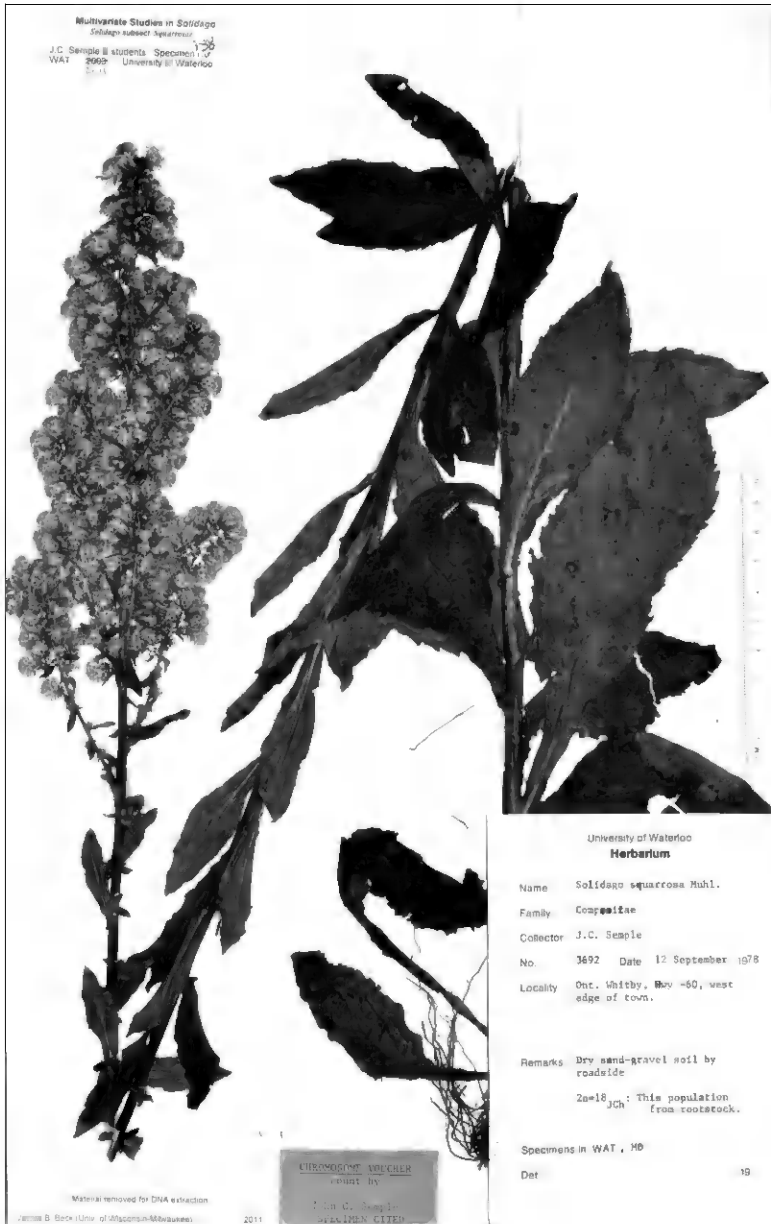
Figure 3. Morphology of *Solidago squarrosa*: *Semple 3692* (WAT) from Whitby, Ontario.

Figure 4. Details of the morphology of *Solidago squarrosa*. **A-C.** Lower, mid and upper stem in inflorescence, *Morton & Venn NA17632* (TRT), Maine. **D-E.** Lower stem leaves, *Semple & B. Semple 11529* (WAT) and *Morton & Venn NA11936* (TRT), New Brunswick and Maine, respectively. **F.** Mid stem leaf, *Morton & Venn NA17632* (TRT). **G.** Head, *Morton & Venn NA17632* (TRT). Scale bars = 1 mm in A-C, and G; = 1 cm in D-F.

Figure 5. *Solidago squarrosa* 1.3 m tall, *Semple & B. Semple 11529* (WAT) in Victoria Co., New Brunswick.

Figure 6. Morphology of *Solidago villosicarpa*: *Semple 11649 C* (WAT) from Brunswick Co., North Carolina.
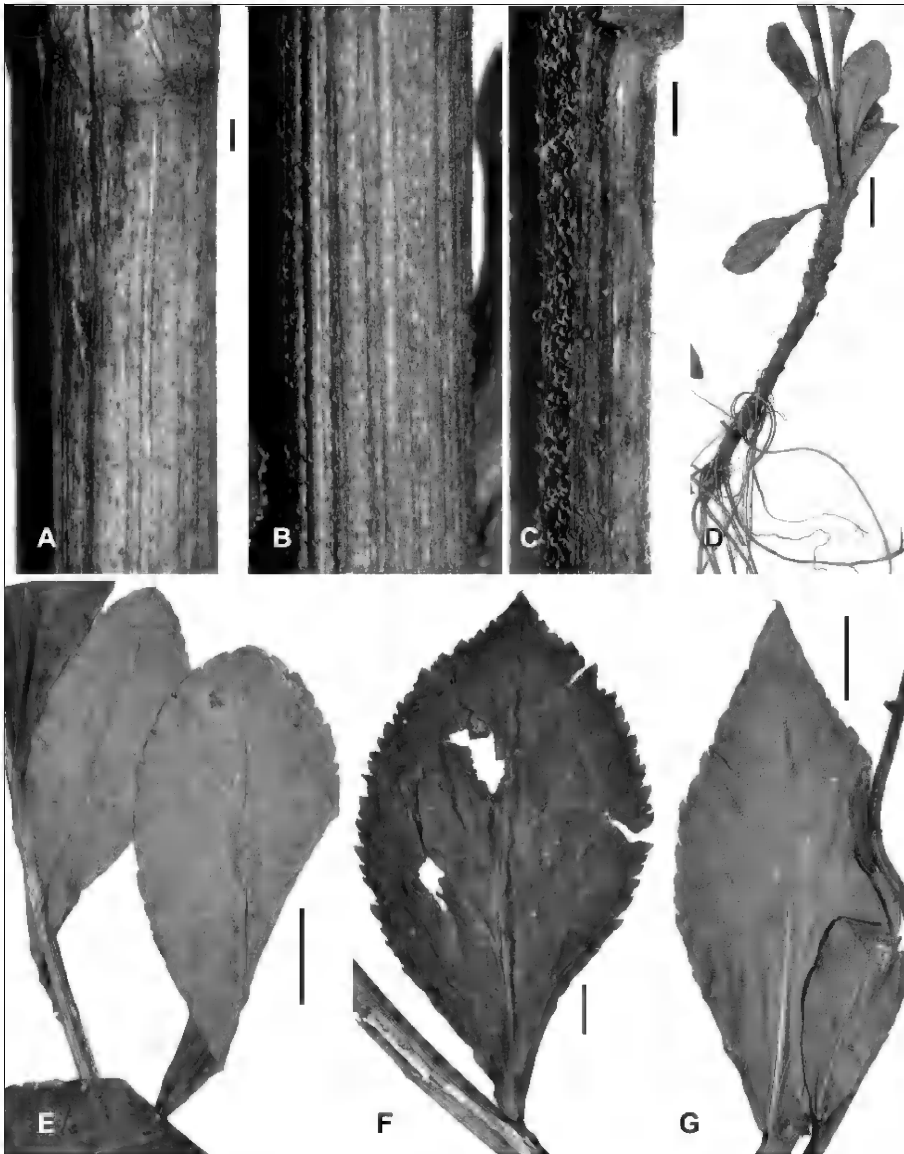
Figure 7. Details of the morphology of *Solidago villosicarpa.* **A-C.** Lower, middle and upper stem in inflorescence, *Semple 11645* (WAT). **D-E.** Portion of rootstock and lower stem leaves of small plant, *Semple 11649 B* (WAT). **F-G.** Mid and upper stem leaves of large plant, *Semple 11645* (WAT). Scale bars = 1 mm in A-C; = 1 cm in D-G.

Figure 8. *Solidago villosicarpa, Semple & C. Tinbrink 11*637 (WAT). **A.** Large plant after rain, USMC Camp Lejune, Onslow Co., North Carolina. **B.** Flowering heads, involucres 5-9–6.2 mm tall.
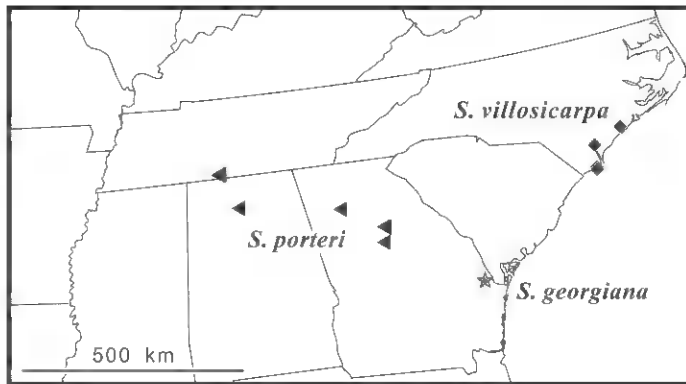
Figure 9. Ranges of distribution of *Solidago georgiana* (yellow star), *S. porteri* (green triangles), and *S. villosicarpa* (black diamonds) and locations of specimens included in the multivariate analyses.
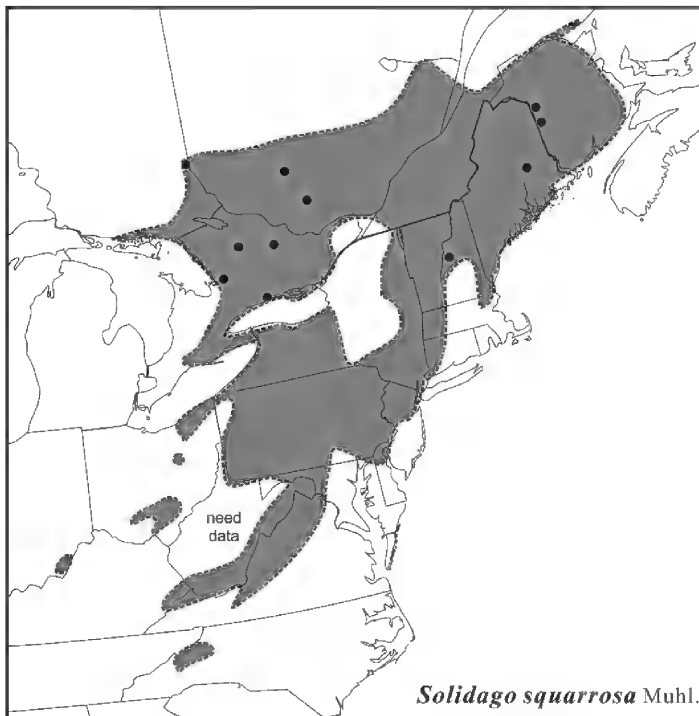
Figure 10. Range of distribution of *Solidago squarrosa* and locations of specimens included in the multivariate analyses.

MATERIALS AND METHODS

In total, 50 specimens from GA, the J.K. Morton personal herbarium now deposited in TRT, NY, TAWES, and WAT in MT (Thiers, continuously updated) were scored and included in the analysis: *Solidago georgiana* (1 unassigned a priori), *S. porteri* (11 specimens), *S. roanensis* (17 specimens), *S. squarrosa* (11 specimens from the northern half of the range), and *S. villosicarpa* (9 specimens). These were selected from more than 300 specimens examined. For each specimen, 18 vegetative and 19 floral traits were scored when possible: 1-5 replicates per character depending upon availability of material and whether or not the trait was meristic (Table 1). Basal rosette leaves were often not present. Lower stem leaves were sometimes not present. Mean values were used in the analyses, while raw values were used to generate ranges of variation for each trait. All traits scored are listed in Table 1.

All analyses were performed using SYSTAT v.10 (SPSS 2000). Details on the methodology are presented in Semple et al. (2016) and are not repeated here. One STEPWISE discriminant analysis was performed on four species level a priori groups (*Solidago porteri*, *S. roanensis*, *S. squarrosa*, and *S. villosicarpa*) with one specimen of *S. georgiana* not included in an a priori group but included in the a posteriori classificatory discriminant analysis.

Table 1. Traits scored for the multivariate analyses of 261 specimens of *Solidago* subsect. *Squarrosae*.

Abbreviation	Description of trait scored
STEMHT	Stem height measured from the stem base to tip (cm)
BLFLN	Basal rosette leaf length including petiole (mm)
BLFPETLN	Basal rosette leaf petiole length (not scored if winged margins broad)
BLFWD	Basal rosette leaf width measured at the widest point (mm)
BLFWTOE	Basal rosette leaf measured from the widest point to the end (mm)
BLFSER	Basal rosette leaf-number of serrations on 1 side of margin
LLFLN	Lower leaf length measured from the leaf base to tip (mm)
LLFWD	Lower leaf width measured at the widest point (mm)
LLFWTOE	Lower leaf measured from the widest point to the end (mm)
LLFSER	Lower leaf dentation-number of serrations of lower leaf
MLFLN	Mid leaf length measured from the leaf base to tip (mm)
MLFWD	Mid leaf width measured at the widest point (mm)
MLFWTOE	Mid leaf measured from the widest point to the end (mm)
MLFSER	Mid leaf dentation-number of serrations of mid leaf
ULFLN	Upper leaf length measured form the leaf base to tip (mm)
ULFWD	Upper leaf width measured at the widest point (mm)
ULFWTOE	Upper leaf measured from the widest point to the end (mm)
ULFSER	Upper leaf dentation-number of serrations of upper leaf
CAPL	Length of inflorescence (cm)
CAPW	Width of inflorescence (cm)
INVOLHT	Involucre height at anthesis (mm)
OPHYLN	Outer phyllary length (mm)
OPHYLW	Outer phyllary width (mm)
IPHYLN	Inner phyllary length (mm)

IPHYLW	Inner phyllary width (mm)
RAYNUM	Number of ray florets per head
RSTRAPLN	Ray strap length top of the corolla tube to the tip of the strap (mm)
RSTRAPWD	Ray strap width measured at the widest point (mm)
RACHLN	Ray floret ovary/fruit body length at anthesis (mm)
RPAPLN	Ray floret pappus length at anthesis (mm)
DCORLN	Disc floret corolla length from the base to tip of the corolla lobes (mm)
DLOBLN	Disc floret corolla lobe length lobe (mm)
DACHLN	Disc floret ovary/fruit body length at anthesis (mm)
DPAPLN	Disc floret pappus length at anthesis (mm)

RESULTS

The Pearson correlation matrix yielded r > |0.7| for most pairs of leaf traits reducing the number to be used to mid and upper stem leaf lengths, mid and upper stem leaf widths, and numbers of mid of upper stem leaf serrations. Basal rosette leaves were often absent and were not included in the discriminant analyses: basal leaf length, basal leaf petiole length, and basal leaf length from widest point to tip were all highly correlated. Lower leaves were sometimes absent and lower leaf traits were excluded from discriminant analyses. Many floral traits also were highly correlated. Involucre height correlated highly with inner phyllary length, ray floret pappus length, disc corolla length, and disc floret corolla length. Outer and inner phyllaries lengths were highly correlated. Inner phyllary length correlated highly with ray floret lamina length, ray floret pappus length, disc floret corolla length and disc floret pappus length. Ray floret lamina length correlated highly with ray floret lamina width, ray floret ovary length, ray floret pappus length, disc floret corolla length, and disc floret pappus length. Ray and disc floret ovary/fruit body lengths at anthesis were highly correlated. Ray floret pappus length correlated highly with disc floret corolla length and disc floret pappus length. Disc floret corolla length correlated highly with disc floret ovary/fruit body length and disc floret pappus length. Outer phyllary length, numbers of ray florets, ray floret lamina width, number of disc florets, disc floret corolla length, and disc floret corolla lobe length were included in the multivariate analysis.

In the STEPWISE discriminant analysis of 50 specimens of four species level a priori groups in (*Solidago porteri*, *S. roanensis*, *S. squarrosa*, and *S. villosicarpa*), the following eight traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: number of ray florets (12.57), disc corolla length (12.44), disc corolla lobe length (10.24), mid stem leaf width (8.46), outer phyllary length (6.40), mid stem leaf length (5.75), number of disc florets (5.71), and upper stem leaf length (4.14). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 2. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between *S. roanensis* and *S. squarrosa* (31.391; the smallest separations were between *S. squarrosa* and *S. villosicarpa* (10.130), *S. porteri* and *S. roanensis* (10.480), and *S. porteri* and *S. villosicarpa* (10.707).

In the Classificatory Discriminant Analysis of the four species level a priori groups (*Solidago porteri*, *S. roanensis*, *S. squarrosa*, and *S. villosicarpa*) plus 1 unassigned specimen of *S. georgiana*,

Table 2. Between groups F-matrix for the four a priori groups analysis (df = 8   38).

Group	*porteri*	*roanensis*	*squarrosa*
roanensis	10.480		
squarrosa	17.429	31.391	
villosicarpa	10.707	21.052	10.130

Wilks' lambda = 0.0156 df = 8 3 45; Approx. F= 14.6488   df = 24 110 prob = 0.0000

percents of correct a posterori assignment to the same a priori group ranged from 91-100%. The Classification matrix and Jackknife classification matrix are presented in Table 3. Results are presented in order of decreasing percents of correct placement. All 9 specimens of the *S. villosicarpa* a priori group (100%) were assigned a posteriori into the *S. villosicarpa* with 100% probability.   All 17 specimens of *S. roanensis* a priori group (100%) were assigned a posteriori to the *S. roanensis* group; 16 specimens with 98-100% probability and 1 specimen with 87% probability (13% to *S. porteri*). Eleven of the 12 specimens of the *S. porteri* a priori group (92%) were assigned a posteriori to the *S. porteri* group: 9 specimens with 99-100% probability, 1 specimen with 92% probability, and 1 specimen with 73% probability (12% to *S. squarrosa*, 10% to *S. villosicarpa*, and 6% *S. roanensis*). One specimens of the *S. porteri* a priori group was assigned a posteriori to the *S. villosicarpa* group with 69% probability (23% to *S. porteri*; *Porter s.n.* NY from Monticello, Georgia; a ca. 30 cm shoot with an inflorescence of only 5 heads; this is the smaller shoot on the lectotype of the species; the larger shoot on the lectotype was assigned a posteriori to *S. porteri* with 100% probability). Ten of the 11 specimens of the *S. squarrosa* a priori groups (91%) were assigned a posteriori to the *S. squarrosa* group with 99-100% probability. One specimens of the *S. squarrosa* a priori group was assigned a posteriori to the *S. villosicarpa* group with 48% probability (28% to *S. squarrosa* and 23% to *S. porteri*; *Semple & Brouillet 3467* WAT from Grafton Co., New Hampshire; the phyllaries are strongly squarrose and the leaves are typical for *S. squarrosa* but the heads had a mean value of only 7 ray florets). The single specimen of *S. georgiana* not assigned to an a priori group was assigned a posteriori to *S. porteri* with 67% probability (23% to *S. roanensis* and 10% to *S. villosicarpa*).

Two dimensional plots of CAN1 versus CAN3 and CAN1 versus CAN2 canonical scores for 50 specimens of *Solidago georgiana* (yellow stars), *S. porteri* (green triangles), *S. roanensis* (open blue stars), S. speciosa (yellow stars), *S. squarrosa* (red star bursts), and *S. villosicarpa* (black diamonds).are presented in Fig. 11. Eigenvalues on the first three axes were 7.458, 2.062 and 1.473.

Table 4. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of four a priori groups; a posteriori placements to groups in rows.

Group	*porteri*	*roanensis*	*squarrosa*	*villosicarpa*	% correct
porteri	11	0	0	1	92
roanensis	0	17	0	0	100
squarrosa	0	0	10	1	91
villosicarpa	0	0	0	9	100
Totals	11	17	10	11	96

Jackknifed classification matrix

Group	*porteri*	*roanensis*	*squarrosa*	*villosicarpa*	% correct
porteri	9	10	0	2	75
roanensis	0	17	0	0	100
squarrosa	0	0	10	1	91
villosicarpa	0	0	0	9	100
Totals	9	18	10	12	92
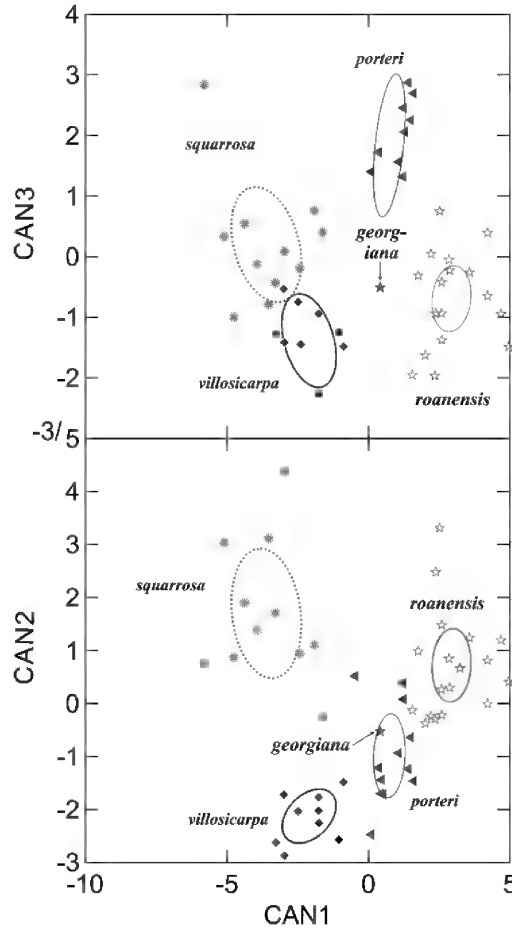
Figure 11. Plot of canonical scores (CAN1 vs CAN3 and CAN1 vs CAN2) for 51 specimens of Solidago subsect. Squarrosae: *S. georgiana* (yellow stars), *S. porteri* (green triangles), *S. roanensis* (open blue stars), S. speciosa (yellow stars), *S. squarrosa* (red star bursts), and *S. villosicarpa* (black diamonds).

DISCUSSION

The results of the multivariate analysis strongly support recognition of *Solidago porteri*, *S. roanensis*, *S. squarrosa*, and *S. villosicarpa as* distinct species. The results also indicate that *S. georgiana* does not fit strongly into the other four species although it is more similar to *S. porteri*. The yellow star symbol for the *S. georgiana* specimen was placed within the 95% confidence ellipse of *S. porteri* on the CAN1 versus CAN2 plot in Fig. 11, but the yellow star symbol for the *S. geogiana* specimen was placed by itself in between the other four species on the CAN1 versus CAN3 plot in Fig. 11. Descriptive statistics on raw data on morphological traits of specimens used in the multivariate analysis of the five species are presented in Table 4.

Solidago georgiana, *S. porteri*, *S. roanensis*, *S. squarrosa*, and *S. villosicarpa* are not likely to be misidentified because each species has a set of distinct features and the ranges are allopatric. *Solidago squarrosa* is the only species in the subsection having long strongly reflexed outer phyllaries tips and cylindrical involucres when fresh. *Solidago porteri* is the only hexaploid in the subsection and has the largest involucres and the longest stem hairs of these five species. *Solidago roanensis* has the smallest heads and is the only species with multi-veined phyllaries. *Solidago villosicarpa* has the most showy heads with its long broad ray laminae and cylindrical involucres with broad appressed phyllaries. The little-known *S. georgiana* has mid-sized involucres with appressed phyllaries; it is the least distinctive of the five species although its ray floret laminae were the widest on average; it is the only one of the five species occurring on the outer coastal plain in southeastern Georgia.

All five species share the glabrous lower stem condition with hairs occurring more densely distally on the mid to upper stem and into the inflorescence. Other species in the subsection are either hairy to the base of the stem or glabrous except in the inflorescence. The length of the stem hairs is shortest in *Solidago roanensis* and longest in *S. porteri*, which may be a gigas effect of the higher ploidy level in the latter species. Whether or not the stem hair distribution feature is a synapomorphy indicating these five species form a clade within subsect. *Squarrosae* needs to be tested using methods suitable for phylogenetic analysis.

Table 4. Descriptive statistics on raw data on morphological traits of specimens used in the multivariate analysis *S. georgiana*, *S. porteri*, *S. roanensis*, *S. squarrosa*, and *S. villosicarpa*: min-**mean**-max; * traits selected in STEPDISC analyses. Abbreviations of traits are described in Table 1.

Trait	*S. georgiana*	*S. porteri*	*S. roanensis*	*S. squarrosa*	*S. villosicarpa*
STEMHT cm	71	34–**71.5**–123	26–**61.2**–101	57.5–**96.1**–129	57–**95**–124
BLFLN mm	–	63	9.5–**93.3**–185	66–**214**–360	90–**131**–173
BLFPETLN mm	–	30	4.5–**48.8**–110	6–**89**–165	0–**38**–65
BLFWD mm	–	18	2.3–**20.4**–36	18–**51.2**–99	25–**40.71**–55
BLFWTOE mm	–	14	2.3–**25.9**–80	29–**51.7**–89	20–**38.3**–53
BLFSER	–	2	4–**10.2**–21	10–**18.4**–33	7–**16.5**–26
LLFLN mm	70–**100**–120	46–**125.4**–249	10.5–**85.6**–150	58–**141.2**–245	30–**87**–124
LLFPETLN mm	25–**30**–35	8–**25**–60	4.5–**48.8**–110	20–**47.8**–98	0–**13.5**–42
LLFWD mm	20–**27.7**–38	14–**28.6**–53	2.4–**20.9**–42	17–**42.3**–85	16–**38.5**–64
LLFWTOE mm	30–**45**–60	10–**44.5**–83	3.4–**31.5**–55	24–**44.4**–70	14–**38**–63
LLFSER	12–**16.7**–227	1–**7.1**–17	5–**11.1**–20	4–**14.5**–28	4–**14.7**–32
MLFLN* mm	30–**41.5**–50	38–**90.7**–169	7–**64.8**–125	48–**85.7**–123	30–**62.7**–96
MLFWD* mm	7–**9.5**–12	8–**20**–38	2–**16.3**–32	9–**24.9**–46	10–**26.7**–50

MLFWTOE mm	16–**20**–25	5–**42.5**–84	2.9–**31.2**–55	20–**34.1**–75	10–**27.3**–52
MLFSER	10–**11.5**–14	0–**4**–10	1–**7.7**–20	3–**9.7**–18	0–**8.6**–26
ULFLN* mm	18–**20.8**–23	20–**41.8**–92	4–**39.9**–81	19–**46.2**–75	17–**36.3**–75
ULFWD mm	4–**4.5**–5	6–**10.5**–23	1–**9.4**–19	4–**12.5**–27	9–**13.4**–34
ULFWTOE mm	9–**10.5**–12	6–**20.9**–50	2–**20.1**–41	9–**11.3**–22	7–**16.1**–37
ULFSER	0–**1.5**–5	0–**0.6**–9	0–**4.2**–14	0–**2.4**–12	0–**1.4**–10
CAPL cm	20	3.6–**15.5**–28	5.2–**16.4**–29.2	18–**33.4**–53.5	10–**30.4**–47
CAPW cm	2.5	2.2–**6.8**–12.8	1.8–**2.8**–7	3–**5**–11.5	1.6–**5.3**–12.4
INVOLHT mm	5–**5.0**–5.1	3.2–**6.1**–9.8	2.3–**3.9**–5.6	4–**6.4**–8.8	4.5–**6.2**–8
OPHYLN* mm	2–**2**–2.1	1.3–**1.95**–3.1	0.5–**1.6**–2.8	2–**2.8**–4.3	1.25–**2.1**–3.3
IPHYLN mm	4.5–**4.7**–4.8	3–**6.0**–8	2.1–**3.4**–4.8	3.9–**5.1**–7	4.3–**4.0**–6.3
RAYNUM*	4–**5**–6	1–**6.2**–9	2–**6**–13	4–**12.1**–20	4–**6.4**–11
RLAMLN mm	3.9–**4.1**–4.5	1.5–**3.0**–4.5	1–**1.9**–3	3–**4.0**–5.4	2–**4.5**–6.3
RLAMWD mm	1.5–**1.62**–1.7	0.3–**0.92**–1.9	0.4–**0.73**–1.6	0.5–**0.95**–1.6	0.7–**1.2**–2.0
RACHLN mm	1.2–**1.27**–1.4	0.8–**1.4**–2.13	0.5–**1.2**–2.1	1.0–**1.8**–2.7	1.2–**2.1**–2.7
RPAPLN mm	3.6–**3.7**–3.8	2.8–**4.21**–6	1.3–**2.3**–3.1	3–**4.1**–4.9	3.2–**4.1**–5.1
DISCNUM*	8–**9**–10	8–**12.2**–17	4–**8.6**–13	8–**15.4**–30	6–**13.2**–21
DCORLN* mm	4.3–**4.56**–4.8	2.3–**4.8**–6.6	2.5–**3.6**–4.9	4.7–**5.5**–6.7	4.1–**5.5**–6.5
DLOBLN* mm	0.7–**0.9**–1.1	0.8–**1.6**–2.8	0.2–**0.8**–1.7	0.7–**0.97**–1.5	0.75–**1.1**–1.25
DACHLN mm	1.1–**1.15**–1.2	0.9–**1.5**–3.3	0.6–**1.2**–2.3	1.3–**1.9**–2.8	1.2–**2.3**–3.6
DPAPLN mm	3.5–**3.65**–3.8	3.9–**4.6**–6	1.5–**2.8**–4.2	3.6–**4.6**–6	3–**4.7**–5.6

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HYDROCOTYLE SIBTHORPIOIDES AND *H. BATRACHIUM* (ARALIACEAE) NEW FOR NEW YORK STATE

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ABSTRACT

Spontaneous populations of *Hydrocotyle sibthorpioides* (lawn marsh pennywort) and *H. batrachium* (Araliaceae) are documented for New York state for the first time. *Hydrocotyle batrachium* is also new to North America. *Hydrocotyle sibthorpioides* was first found in 2013 in Queens county; *H. batrachium* was first found in 2016 in Westchester county. Both species are native to eastern Asia and show potential to be aggressive invaders in southeastern New York, particularly in wetlands. A key to the species of *Hydrocotyle* in New York State is provided.

Prior to this report four species of *Hydrocotyle* were known from New York state, all of them native and all but one state-listed rarities: *H. umbellata* – Rare; *H. verticillata* var. *verticillata* – Endangered; and *H. ranunculoides* – Endangered (Young 2010). Among the native New York species, only *H. americana* occurs in abundance in the state. It is the only species historically reported for New York City and has not been documented for New York City since 1901.

The present report documents two additional species for the New York flora, both native to Asia and naturalized in southeastern New York. Fertile herbarium specimens and DNA samples were obtained for all cited specimens and are available for analysis.

Hydrocotyle sibthorpioides Lam.
Spontaneous populations of *Hydrocotyle sibthorpioides* in New York were first detected and identified in Queens County by Nick Wagerik in the summer of 2013. The plants were found on 34th and 35th avenue between 82nd and 81st Streets but not collected. Eve Levine subsequently found spontaneous populations on West 70th St in New York County (Manhattan). In 2014, Levine, the author, Richard Lieberman and Regina Alvarez documented the West 70th Street plants with herbarium specimens and DNA samples. Later that year, the author found *Hydrocotyle sibthorpioides* in Kings County (Brooklyn) and Eve Levine found additional populations in New York County.

The New York plants are glabrous perennial herbs, prostrate and matted; stems slender, rooting at the nodes; leaves usually 2 per node, unequal, the blades basifixed, orbicular or reniform, weakly 7-lobed to merely crenate margined, 0.6–1(-2) cm broad, the basal sinus narrow, < 1/4 circumfrence of the blade, the main veins 7; umbels solitary, with 8–10 flowers, the peduncles about as long as the petioles; fruit 1.5 mm long. Figure 1.

New York. New York Co.: New York City, Upper West Side, 205 W 70th St, between 69th and 70th Streets, 40.778210, -73986567 (WGS84, ±25 m), ca 18 m elev, 16 Sep 2014, *Atha, Alvarez, Levine and Lieberman 14919* (NY); 40.778172, -73985990 (WGS84, 25m), ca 18 m elev, 16 Sep 2014, *Atha, Alvarez, Levine and Lieberman 14921* (NY); 40 9th Ave, between 59 and 60th Streets, 40.769374, -73.984448 (WGS84, ±25m), ca 24 m elev, 17 Sep 2015, *Atha 15288* (NY). Kings Co.: New York City, Brooklyn, Eastern Parkway and Washington Avenue, 40.671531, -73.962694 (WGS84, ±25m), 47 m elev, 14 Oct 2014, *Atha 14936* (NY). Westchester Co.: Tuckahoe, Bronxville Lake on the Bronx River, E shore,

W of Kensington Road and N of Avon Road, 40.947572, -73.832933 (WGS84, ±25m), ca 30 m elev, 24 Sep 2016, *Atha, Nolan and Andruk 15814* (NY).

The New York County collection, *Atha et al. 14919*, was growing in the cracks of a concrete patio and in the adjacent concrete planter with cultivated *Rosa*, *Spirea*, *Buddleja*, *Syringa*, *Hydrangea*, and the weedy species *Potentilla indica* and *Acalypha australis*. The plants were in partial shade and rather sparse, probably due to the frequent trampling and maintenance of the ornaments. The other collection from nearby at the same address (*Atha et al. 14921*) was growing in partial shade in a flat, well-maintained, irrigated lawn planted with *Crataegus* and *Malus*. The plants were very dense and formed nearly a complete covering, competing only with *Potentilla indica*. Less than one mile away, also in Manhattan, the species was found growing in a mostly bare foundation planter at ground level planted with a small *Picea* tree (*Atha 15288*). The site received ample irrigation and partial sun. In a fenced area around the corner, on West 60th St (not vouchered), there was a complete carpet of *Hydrocotyle sibthorpioides* in an irrigated street-level bed about 50 meters square in mostly shade.

The Kings County plants (*Atha 14936*) were growing in a recently installed, well-irrigated lawn contained in architectural boxes at street level in partial sun.

The Westchester County plants (*Atha et al. 15814* and Figure 1) were growing on the floodplain of the Bronx River in wet, silty soil maintained as lawn and used for recreation and visited frequently by Canada geese (*Branta canadensis*).

Hydrocotyle sibthorpioides is native to eastern Asia in wet valleys, grassy areas, and stream banks (She et al. 2005). In North America it is reported from mostly isolated counties from Louisiana and Arkansas northeast to New Jersey and disjunct in California (USDA NRCS 2017). *Hydrocotyle sibthorpioides* has been in North America at least since about 1900 (Britton & Brown 1913). The northernmost North American populations previously known were Hunterdon and Mercer counties in New Jersey (USDA NRCS 2017). In North America it has been found in greenhouses, nurseries, lawns, sidewalks, and shorelines of brackish and fresh water. *Hydrocotyle sibthorpioides* is used as an ornamental ground cover and is sold for the aquarium and terrarium trade (Planted Aquariums Central 2016).

Hydrocotyle batrachium Hance

In October of 2014, the author observed an extensive and well-established population of an unrecognized small-leaved *Hydrocotyle* in a garden bed in suburban Westchester County that upon examination and comparison with herbarium material and floristic treatments, was determined to be *H. batrachium*. In 2016, the same taxon was found and collected on the floodplain of the Bronx River while surveying for the invasive *Corydalis incisa* with Suzanne Nolan and Christina Andruk. *Hydrocotyle sibthorpioides* was also found growing a few meters away in the same floodplain.

The New York plants are glabrous perennial herbs, prostrate and matted; stems rooting at the nodes; leaves usually 2 per node, unequal, the blades basifixed, depressed orbicular, strongly 5-lobed, 0.5–0.8 × 0.6–1.1 cm, the basal sinus wide, > 1/4 circumference of the blade, the main veins 5, sinuses of the lobes reaching about to the middle of the blade; umbels solitary, with 3–4 flowers, the peduncles about as long as the petioles; fruit 2 mm long. Figure 2.

USA. New York. Westchester Co.: New Rochelle, Wood Hollow Lane, 40.942913, -73775002 (WGS84, ±25m), ca 44 m elev, 1 Oct 2014, *Atha, Schuler and DelTorto 14932* (NY); Tuckahoe, Bronxville Lake on the Bronx River, E shore, W of Kensington Road and S of Avon Road, 40.945733, -73.834539 (WGS84, ±25m), ca 30 m elev, 24 Sep 2016, *Atha 15821* (NY).

The Wood Hollow Lane plants (*Atha et al. 14932*) were growing in a well-irrigated ground-level planter in partial sun from which a dense patch of *Pachysandra terminalis* had recently been removed. The gardener reported never having seen the *Hydrocotyle* until the *Pachysandra* was removed. The Bronx River population (*Atha 15821* and Figure 2) was found on the floodplain of the Bronx River in wet, black silty soil in filtered shade of *Alnus glutinosa*, frequented by *Branta canadensis* (Canada goose).

Hydrocotyle batrachium is native to eastern Asia, ranging from northern Vietnam, central and southern China, Taiwan and the Ryukyu Islands, in open wet areas and grasslands (She et al. 2005; Flora of Taiwan Editorial Committee 1993). *Hydrocotyle batrachium* is reported as *H. sibthorpioides* Lam. var. *batrachium* (Hance) Hand.-Mazz. ex R.H. Shanas in the Flora of China (She et al. 2005). The taxon is treated at the species level as *H. batrachium* in the flora of Taiwan (Flora of Taiwan Editorial Committee 1993) and Eichler's comprehensive review of the genus (Eichler 1987a).

Key to *Hydrocotyle* species in New York State

1. Leaves peltate.

    2. Inflorescences umbellate, the umbels solitary .... **Hydrocotyle umbellata**
    2. Inflorescences verticillate, the verticels several, interrupted .... **Hydrocotyle verticillata**

1. Leaves basifixed (not peltate).

    3. Leaves (1-)2–7 cm broad; umbels sessile or the peduncles < 1/2 length of petioles.

        4. Umbels sessile or subsessile .... **Hydrocotyle americana**
        4. Umbels pedunculate .... **Hydrocotyle ranunculoides**

    3. Leaves 0.6–1.5(-2) cm broad; umbels pedunculate, the peduncles > 1/2 length of petioles.

        5. Leaves nearly orbicular with 7 principal veins and usually 7 principal lobes, the basal sinus narrow, < 1/4 circumference of the blade; umbels with 8–10 flowers; fruit 1.5 mm long
        .... **Hydrocotyle sibthorpioides**
        5. Leaves compressed oblong with 5 principal veins and 5 principal lobes, the basal sinus broad, > 1/4 circumference of the blade; umbels with 3–4 flowers; fruit 2 mm long
        .... **Hydrocotyle batrachium**

Examination of both species in the field and from the many herbarium specimens preserved in the NY and BKL herbaria shows that *Hydrocotyle sibthorpioides* and *H. batrachium* are each consistent morphologically as described here and are consistently distinct from one another (see key above). Both taxa were found growing together in the same habitat in Westchester county and no intermediates were found.

Background

Hydrocotyle is a nearly cosmopolitan genus provisionally placed in the Araliaceae (Plunkett et al. 2004; Yi et al. 2004; Plunkett & Nicolas 2009, but see Konstantinova & Yembaturova 2010). In 1820, Achille Richard published the first and only worldwide monograph of the genus (Mathias 1936). In 1987, Hansjorg Eichler published a nomenclatural and bibliographic survey of the genus (Eichler 1987a, b, c) providing the only global treatment of the genus since the monograph of Richard. Since Eichler's review, only regional revisions and floristic treatments have been published and the genus is greatly in need of revision (Konstantin & Yembaturova 2010). There are approximately 100 currently accepted species (Pimenov & Leonov 1993; She et al. 2005; Du & Ren 2010; The Plant List 2017).

Prior to the present work, nine species of *Hydrocotyle* were known from North America, six native and three non-native: *H. americana* L., *H. bonariensis* Comm. ex Lam., *H. bowlesioides* Mathias & Constance – non-native, *H. moschata* G. Forst.– non-native, *H. prolifera* Kellog, *H. ranunculoides* L. f., *H. sibthorpioides* Lam.– non-native, *H. umbellata* L., and *H. verticillata* Thunb. (USDA NCRS 2017).   The Central American species *H. bowlesioides* was added to the North American flora in 1983 (Anderson 1983).

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Figure 1. *Hydrocotyle sibthorpioides* on floodplain of the Bronx River, Westchester County, New York (*Atha et al. 15814*). Note narrow sinuses of leaf blades and umbels with 8–10 flowers.

Figure 2. *Hydrocotyle batrachium* on floodplain of the Bronx River, Westchester County, New York (*Atha 15821*). Note open sinus of leaf blades and umbels with 3–4 flowers.

NATURALIZED OCCURRENCE
OF *RUELLIA DIPTERACANTHUS* (ACANTHACEAE) IN THE USA

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ABSTRACT

Ruellia dipteracanthus (Nees) Hemsl. is reported as naturalized in the USA, from Broward Co., Florida, and Harris Co., Texas. The Texas population occurs along an ephemeral drainage in a secondary successional pine-hardwood forest. The population of ten plants probably has been introduced from garden plants in adjacent residential areas. This species can be distinguished by its low-growing, ground-covering habit, exhibiting simple, lanceolate and pubescent leaves with arcuate venation.

The present paper documents the first recorded occurrences of *Ruellia dipteracanthus* outside of cultivation in the USA (USDA, NRCS 2017; Kartesz 2017; Turner 1991; Turner et al. 2013). The Texas plants, from Harris Co., occur approximately 950 miles north of the nearest known wild populations in Mexico (Hemsley 1882). The population consisted of ten flowering plants growing in the bottom of an ephemeral drainage. The Florida voucher is a specimen at the University of South Florida herbarium (USF) (Wunderlin et al. 2017). This species can be easily distinguished by other species of *Ruellia* in Texas by its low-growing, ground-covering habit and pubescent leaves with arcuate venation (Mowat 2017) (Figure 1).

Ruellia dipteracanthus (Nees) Hemsl. (syn. *Ruellia pohlii* Lindau)

Florida. Broward Co.: Secret Woods Nature Center, Dania Beach, T50S, R42E, Sec. 20, 19 May 2001, *Howell 413* (USF, digital image!). **Texas**. Harris Co.: Piney Point Village (west Houston), drainage S of intersection of Memorial Dr. and Briar Forest Dr., 29.75086162° -95.52580442, bottom of a drainage over sandy soil mixed with concrete and bricks, secondary successional forest under a canopy of *Quercus virginiana, Celtis laevigata, Ulmus alata, Acer negundo, Sapium sebiferum, Quercus nigra,* and *Ilex vomitoria,* 15 Apr 2017, *Keith 1123* (SHST). Figure 1.

The Texas collection locality is in Piney Point Village, part of a collection of residential communities in west Houston known as Memorial Villages, an area of over ten square miles. Buffalo Bayou, a slow-moving, natural spring-fed river and the principal river of Greater Houston, runs through Memorial Villages. The area consisted of large country estates and farmland until the construction of the Addicks Reservoir in the 1940s and the Barker Reservoir in the 1950s. Buffalo Bayou was channelized soon after, and the region was gradually annexed into Houston (TSHAonline 2010).

Ruellia dipteracanthus is likely introduced from cultivated plants in adjacent residential areas from home gardens or other parts of the community. It is a popular cultivated ornamental plant in Mexico and is a native of Cerrado vegetation in Brazil (Mowat 2017; Nees 1847). A second specimen from Florida appears to be cultivated (Wunderlin et al. 2017).

Wild petunias of the genus *Ruellia* include approximately 150 species found mainly in tropical areas of the world. BONAP and The Plants Database show 19 native species of *Ruellia* in the USA; *Ruellia dipteracanthus* brings the list of non-native, invasive wild petunias recorded outside of cultivation in the USA to 3, also including *R. caerulea* Morong (syn. *R. simplex* C. Wright) and *R. ciliatiflora* Hook. (Turner 1991; Kartesz 2017; USDA, NRCS 2017).

Figure 1. *Ruellia dipteracanthus* at the collection site in Harris County. Photo by Eric Keith.

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STUDIES IN NEOTROPICAL COMPOSITAE–XII.
PIPTOCARPHA CARDENASII (VERNONIEAE), A NEW SPECIES OF SUBGENUS *PIPTOCARPHA* SERIES *ASTEROTRICHIAE* FROM CAQUETA, COLOMBIA

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ABSTRACT

Piptocarpha cardenasii Pruski, **sp. nov.** (Compositae: Vernonieae: Piptocarphinae), a new species from Caquetá, Colombia is described, and its distinguishing features depicted. By its pointed, sclerified anther tails the new species is referred to subgenus *Piptocarpha*, and by its concolorous, loosely stellate-pubescent leaf blades we place *P. cardenasii* in the formerly monotypic, pluriflorous, paleate-capitulate series *Asterotrichiae*. The obovate leaves, non-costate phyllaries, and open capitulescences with mostly pedunculate capitula distinguish *P. cardenasii* from Peruvian-centered *P. asterotrichia*, the type of the series.

Piptocarpha R. Br. (Compositae: Vernonieae: Piptocarphinae) is a traditionally recognized genus (e.g., Candolle 1836; Schultz Bipontinus 1863, as synonymous *Carphobolus* Schott ex Sch. Bip.; Baker 1873; Bentham & Hooker 1873; Hoffmann 1890–1894) characterized by apically rounded stylar papillae (Fig. 1A) and deciduous mid-series and inner phyllaries. Smith and Coile (2007) revised *Piptocarpha* and recognized 46 species (44 of these are endemic to South America — including Trinidad —, one ranges from South America to southern Mexico, and one is a Puerto Rican endemic) distributed in two more or less equally speciose subgenera. They characterized Brazilian-centered *Piptocarpha* subg. *Hypericoides* (Sch. Bip.) G. Lom. Sm. as having blunt, broad-based anther tails (Fig. 1B–C), and widespread *Piptocarpha* subg. *Piptocarpha* as having pointed, sclerified anther tails (Figs. 2B, 3A).

Piptocarpha was placed in subtribe Piptocarphinae by Robinson et al. (1980), and the component genera of the subtribe are more or less those recognized by Robinson et al. (1980), Pruski (1992, 1996, 1997, 2016), and Robinson (1989, 1999, 2006). The few Vernonian genera similar to *Piptocarpha* in gestalt and by their deciduous inner phyllaries include *Critoniopsis* Sch. Bip. (Robinson 1993), *Cuatrecasanthus* H. Rob. (Robinson 1989), *Eremosis* (DC.) Gleason (Pruski 2016), and *Piptocoma* Cass. (Pruski 1996). Each of these four genera, however, have narrow-tipped stylar papillae unlike *Piptocarpha*, and none have the pointed, sclerified anther tails that characterize *Piptocarpha* subg. *Piptocarpha*. This subgenus is the only Compositae group with such anther tails and is recognizable at a glance.

Explorations in Amazonian Colombia, coordinated by Dairon Cárdenas of the Instituto Amazónico de Investigaciones Científicas (SINCHI), have resulted in discovery of a new species of Compositae with pointed, sclerified anther tails (Figs. 2B, 3A) and concolorous, loosely stellate-pubescent leaves (Figs. 4, 5A, 6). This new species was determined as *Piptocarpha* sp. by Dr. Santiago Diaz-P. (1944–2014) and is described here as *P. cardenasii* Pruski, which we place in *Piptocarpha* subg. *Piptocarpha*. Forty-eight species of *Piptocarpha* are now recognized, the 46 by Smith and Coile (2007), Brazilian *P. longipedunculata* Volet (of subgenus *Hypericoides*; Volet et al. 2017; as the excluded *P. obovata* in Smith & Coile 2007: 80), and Colombian *P. cardenasii*.

A majority of the 48 species have conspicuously discolorous leaves with relatively small, axillary capitula (Smith 1982), but a few species have easily observed, distinctly different morphologies, being concolorous-leaved, terminal-flowered, relatively large-capitulate, pedunculate, and/or paleate-capitulate. *Piptocarpha cardenasii* by its concolorous leaves somewhat resembles several Brazilian, Peruvian, and Venezuelan species but matches none (viz Baker 1873; Gleason 1932; Cabrera 1944, 1974; Cuatrecasas 1955; Aristeguieta 1964; Cabrera & Klein 1980; Jones 1980; Smith 1981, 1982; Badillo 1989; Pruski 1997, 2010, 2013; Nakajima et al. 2001; Robinson 2002; Smith & Coile 2007; Grokoviski et al. 2009; Pruski & Funston 2011). *Piptocarpha cardenasii* is especially distinctive by its concolorous, loosely stellate-pubescent abaxial leaf blade surfaces and relatively large, pluriflorous, paleate, mostly conspicuously pedunculate capitula (Figs. 4, 5A, 6).
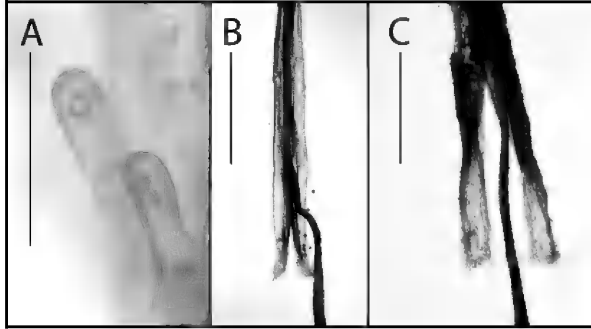
Figure 1. Select microfeatures of *Piptocarpha*. A. Apically rounded stylar papillae characteristic of *Piptocarpha*; cross walls are not at all evident. B–C. Broad non-sclerified anther tails of subg. *Hypericoides*. The dark-staining filament is in the bottom-center of each image. (A–B *P. sellowii* (Sch. Bip.) Baker, *Zardini & Velázquez 13002*, MO; C *P. geraldsmithii*, *Jaramillo et al. 498*, MO). [Scale bars A 75 μm, B 0.6 mm, C 0.3 mm].
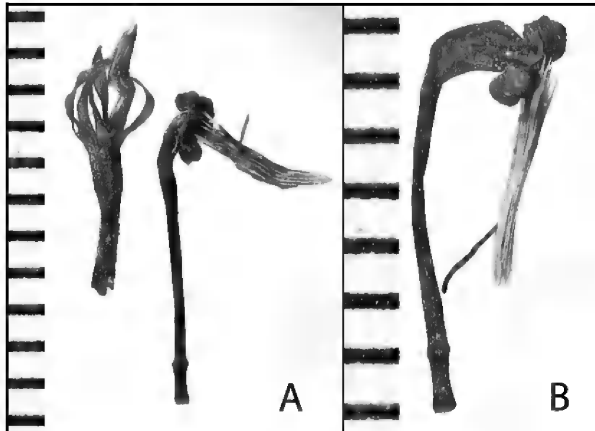
Figure 2. *Piptocarpha cardenasii*, florets showing dark-drying corollas and stramineous anthers (cypselae and pappus bristles removed). The corolla tubes are bulbous proximally where surrounding stylar nodes. A. Corollas showing elongate tube, throat, and lobes. B. Corolla, style trunk, and downturned anthers with tails directed upwards. (*Correa 7052*, COAH). [A metric ruler is on the left of each image].
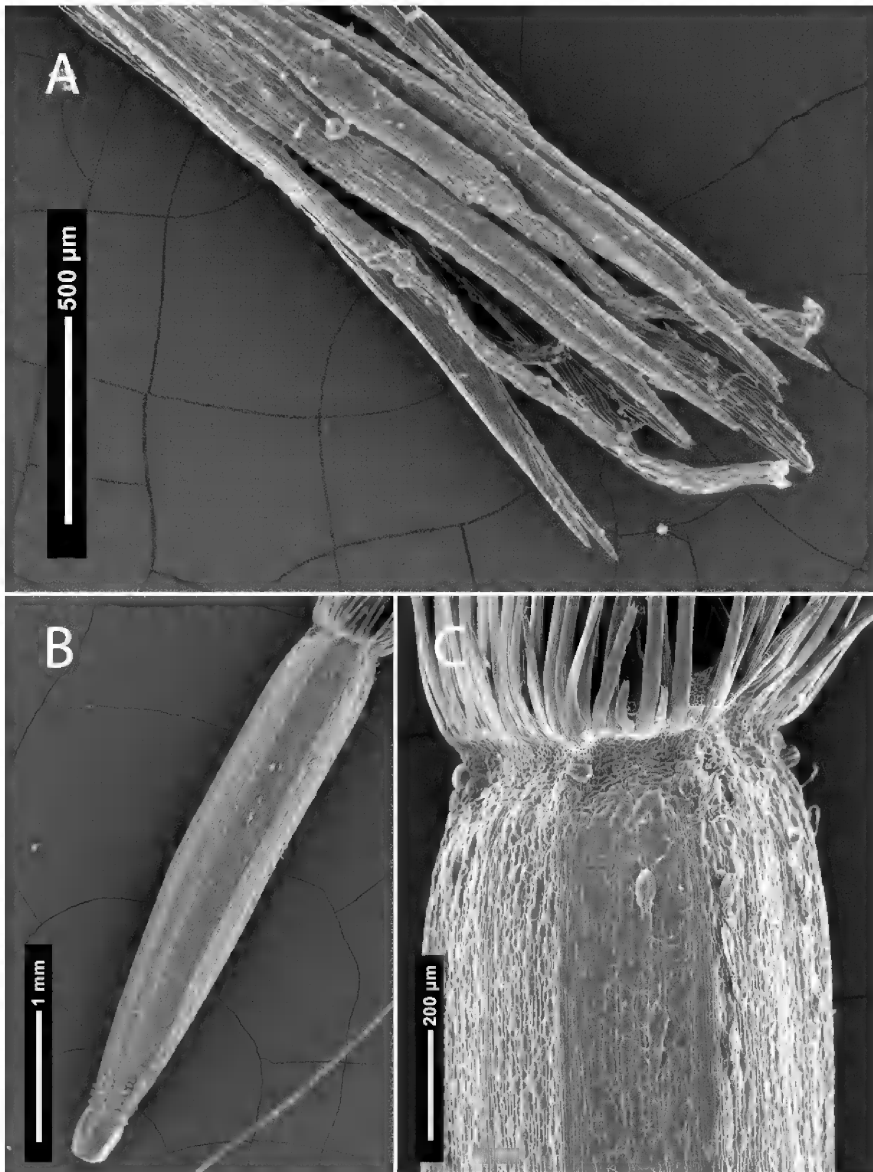
Figure 3. SEM micrographs of *Piptocarpha cardenasii*. A. Anther base showing pointed, sclerified tails. The tails of adjacent thecae are appressed and the filaments are curved at tips where dissected. B. Cypsela showing symmetric carpopodium. C. Cypsela showing distal glands and pappus bristle bases; the cypselae are 4–5-angled and 10-striate. (*Cardenas et al. 44409*, COAH).
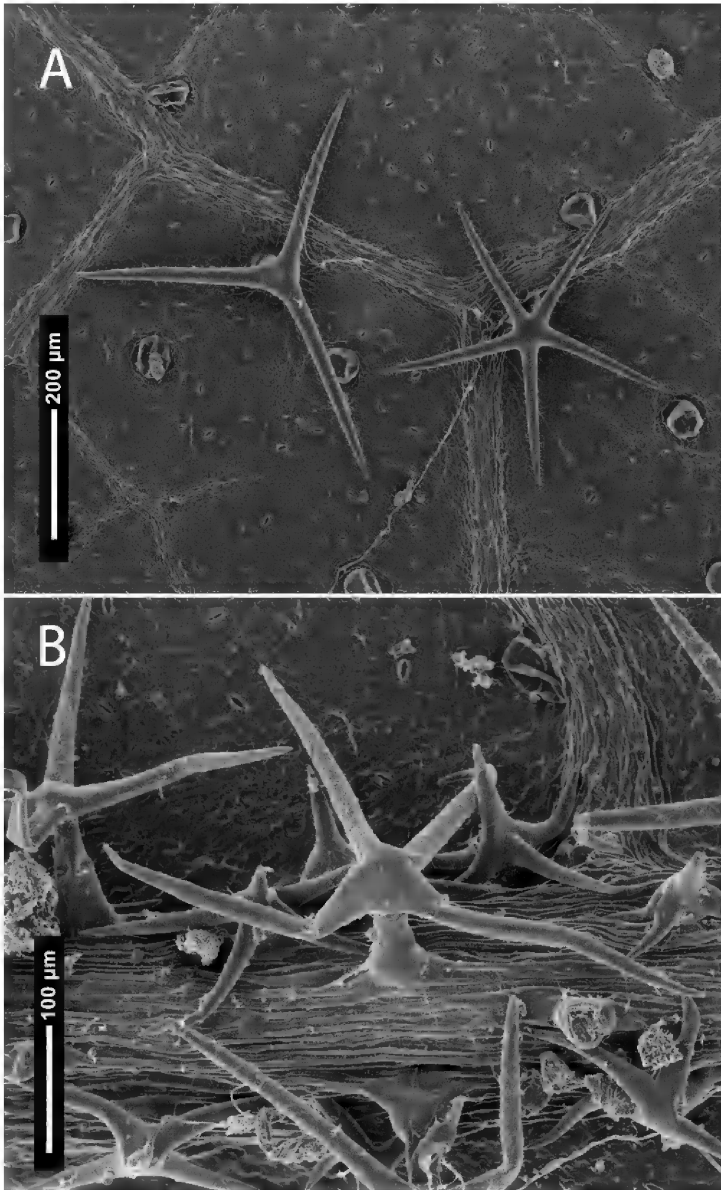
Figure 4. SEM micrographs of stellate trichomes on abaxial leaf blade surfaces of *Piptocarpha cardenasii*. A. Trichomes (3-armed towards the left and 5-armed towards the right) as seen from above. B. Side view of 4-armed trichome on leaf vein showing the short, but distinct stipe. (*Cardenas et al. 44409*, COAH).

Figure 5. Flowering branches of *Piptocarpha* subg. *Piptocarpha* ser. *Asterotrichiae*. A. *Piptocarpha cardenasii* showing mostly pedunculate capitula in open cymose distal capitulescences; on occasion a few subsessile capitula are found. B. *Piptocarpha asterotrichia* showing leafy stem and sessile (larger than usual) capitula in glomerulate capitulescences in two distal nodes. (A *Cardenas et al. 44409*, type collection; B *Croat et al. 84362*, unmounted duplicate). [A metric ruler is positioned at the bottom of the plate].

PIPTOCARPHA CARDENASII Pruski, **sp. nov. TYPE: COLOMBIA. Caquetá**. Mun. San Vicente del Caguán, Inspeccion Guacamaya, vereda La Música, río Caguán, 2° 20' 46" N, 74° 54' 12" W, 600 m, 12 July 2015, *D. Cárdenas*, *Castaño*, *Rodríguez*, *Marin*, *Restrepo*, *Paky*, *Perdomo & Paky 44409* (holotype: COAH; isotype: MO). Figs. 2–4, 5A, 6–8.

Frutex scandens circiter 2+ m alta; folia alterna petiolata, lamina oblonga 12–22 × 6–12 cm concolorata pubescentia pilis stellatis et breviter stipitata pinnatim venosa base cuneata apice obtusa vel rountundata, petiolo 1–2 cm longo; capitulescentia laxe cymosa terminalis et axillares 2–13-capitulata, pedunculi ca. 1 cm longi; capitula discoidea paleacea; involucrum turbinato-pyriformis 12–14 × 5–7 mm; phyllaria imbricata 6–8-seriata; flosculis 17–20; corollae infundibularis 9.5–11.5 mm longae quinquelobatae parce glandulosae; cypselae obconicae circiter 4.5 mm longae; squammae pappo circiter 50–60, 7.5–8 mm longae.

Vining shrubs ca. 2+ m tall; stems subterete and only slightly angled-sulcate distally, closely stellate-pubescent, trichomes moderately dense, loosely-leaved with leaves much longer than distal internodes. **Leaves** alternate, petiolate; petiole 1–2 cm long; blade broadly(-narrowly) obovate, mostly 12–22 × 6–12 cm, stiffly chartaceous or subcoriaceous, pinnately veined with 7–10 larger secondary veins per side, midrib distinctly thicker than the thin secondaries, third order reticulations not very prominent, surfaces basically concolorous, adaxial surface sparsely stellate-pubescent,

abaxial surface moderately stellate-pubescent, trichomes with 3–5 subequal arms 150–250 μm long, arms much longer than the ca. 50 μm long ca. 3-celled stipe, trichome arms not interwoven, also minutely glandular, blade base cuneate, oblique, margins entire, apex obtuse to rounded, with small mucro. **Capitulescences** of loose, open cymes mostly terminating branches, sometimes in leaf axils from the distal-most few nodes, nodes 2–13-capitulate, capitula free, pedunculate from stem or sometimes on common anthophore to ca. 1 cm long, individual peduncles to ca. 1 cm long, usually nearly as long as capitula, on occasion a few subsessile capitula are found. **Capitula** large, discoid, to 20 × 6 mm, moderately long-pedunculate; involucre turbinate-pyriform, 12–14 × 5–7 mm, constricted apically at maturity; phyllaries imbricate, markedly graduate, 6–8-seriate, moderately stiff-indurate, apex acute to acuminate, never strongly costate-apiculate; outer phyllaries triangular-lanceolate, 1–1.5 × 0.7–1.4 mm, moderately spreading especially when pressed, decurrent on proximal portions of elongate-clavate clinanthium, closely matted, cinereous, stellate-pubescent throughout or nearly so, quickly grading to the inner ones; inner phyllaries ovate to lanceolate, 9–11 × 3–5 mm, inserted ca. 2 mm distal to outer phyllary bases, appressed, deciduous post-anthesis, sometimes drying cymbiform, tan proximally where overlapping, dark-purplish in distal half (at least in herbarium specimens), margins broad, glabrous, apex closely matted stellate-pubescent in elongate distal mid-zone, trichomes cinereous, not obviously stipitate; clinanthium flat on top, ca. 2 mm diam., paleate, clinanthial stipe ca. 2 mm long, paleae 10–12.5 × 0.9–1.3 mm, lanceolate, readily deciduous, somewhat conduplicate proximally, becoming narrower and flat distally, hyaline, apex sometimes cinereous-pubescent, sometimes also with a linear-filiform ennation ca. 11 mm long. **Florets** 17–20; corolla 9.5–11.5 mm long, funnelform, moderately 5-lobed, tube elongate, lobes about as long as throat, pale lavender, sparsely glandular especially on throat, otherwise subglabrous, tube narrowly cylindrical, 6–6.5 mm long, bulbous proximally where surrounding stylar node, broadening into throat 1.5–2 mm long, lobes 2–3 mm long, ascending or spreading at anthesis, recurved when dried; anthers ca. 4.5 mm long, tan, caudate, apical appendage eglandular, anther collar cylindrical 0.4–0.5 mm long, about the same diameter as the filaments, tails ca. 0.8 mm long, pointed, sclerified, narrowly acuminate, tails of adjacent thecae appressed but free at the ends; pollen tricolporate, non-lophate, colpae broad; style base nodular, free, held above nectary on narrow stipe, trunk distally long-papillose, branches slender, ca. 2.3 mm long, long-papillose, papillae rounded at apex, stigmatic surface continuous. **Cypselae** 4–5-angled-obconical, ca. 4.5 mm long, 10-striate, brown, sparsely glandular proximally and distally, sparsely setulose distally on faces between striations, also with many embedded resinous idioblasts, pericarp cells with raphide crystals, carpopodium annual, ca. 0.2 mm long, stramineous; pappus 1–2-seriate but outer bristles never squammose and the pappus not markedly double, of 50–60 pale white narrow slightly unequal bristles, mostly 7.5–8 mm long, the longest bristles nearly twice as long as cypselae and somewhat broad-tipped, contiguous basally. **Chromosome number** unknown.

Paratype: COLOMBIA. **Caquetá**. Mun. Florencia, Corregiminto Caraño, R.N. Comunitaria El Manantial Coordenadas, [ca. 1° 38' 06" N, 75° 34' 58" W], s. elev., 2 May 2010, *M. Correa 7052* (COAH).

Distribution and ecology.   *Piptocarpha cardenasii* is known from only the two cited collections (the type and an earlier collected, less complete paratype) from western Caquetá, Colombia (Fig. 8). This vining shrub flowers in May and July and has been collected at about 600 meters elevation. The species grows in foothills of the eastern cordillera of the Andes and should be looked for in adjacent Ecuador and Peru.

Eponymy.   *Piptocarpha cardenasii* is dedicated to Dairon Cárdenas of the Instituto Amazónico de Investigaciones Científicas (SINCHI), director del herbario COAH, collector of the type material, and long-time student of the flora of Amazonian Colombia.
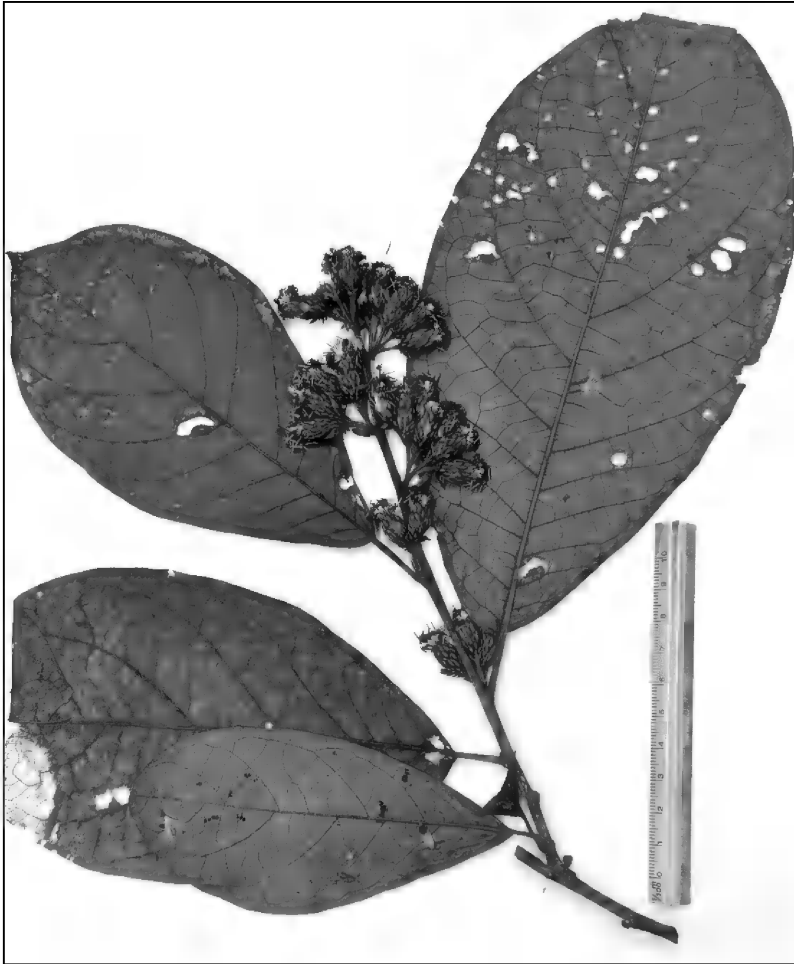
Figure 6. Type collection of *Piptocarpha cardenasii* showing the obovate leaf blades with surfaces basically concolorous and loosely stellate-pubescent (i.e., not cinereous-tomentose abaxially). (*Cardenas et al. 44409*). [A metric ruler is on the right].

The few regional concolorous-leaved species of *Piptocarpha* subg. *Hypericoides* each differ from the new species in anther tail structure as well as by their closely lepidote abaxial leaf blade surfaces. Regional concolorous-leaved species of *Piptocarpha* subg. *Piptocarpha* include axillary-flowered Peruvian *P. canescens* Gleason, axillary-flowered Peruvian and Ecuadorian *P. klugii* G. Lom. Sm. ex H. Rob., axillary-flowered Colombian *richteri* Cuatr., and terminal-flowered Peruvian and Ecuadorian *P. vasquezii* H. Rob. Each of these latter four species was placed by Smith and Coile (2007) in *Piptocarpha* subg. *Piptocarpha* sect. *Oocephalus* and is characterized by 6-flowered capitula, thus differing from pluriflorous *P. cardenasii*.
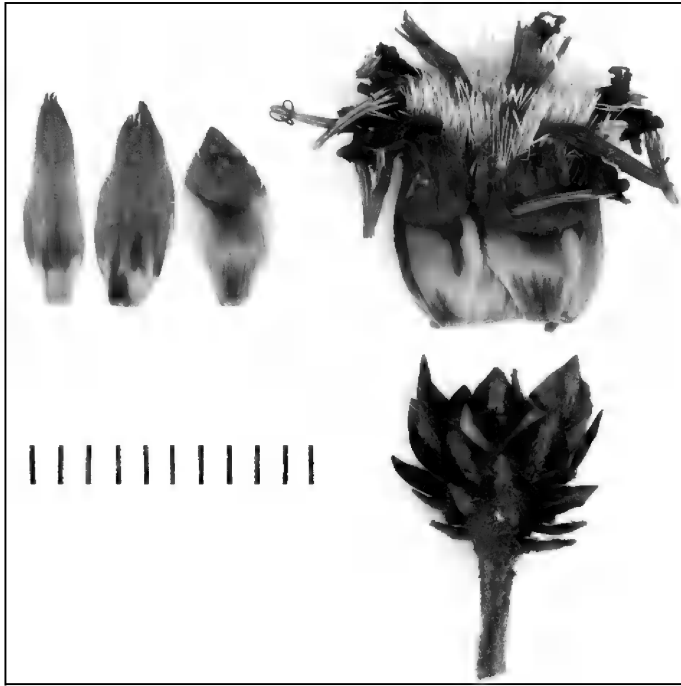
Figure 7. Dissected capitulum of *Piptocarpha cardenasii*, showing (counterclockwise from lower right) involucre with persistent outer phyllaries, detached inner phyllaries with included florets, and three mid-series phyllaries. Deciduous inner phyllaries are characteristic of the genus. (*Cardenas et al. 44409*). [A metric ruler is in the lower left].

The second of two sections of subg. *Piptocarpha* recognized by Smith and Coile (2007) is sect. *Piptocarpha*, within which they recognize four series. Two of these four series are either trees or very thin-leaved, and thereby neither can accommodate *P. cardenasii*. The most common species of either of these two series is *P. rotundifolia*, which has densely stellate-pubescent (not matted-pubescent) leaves with erect, long-stipitate stellate trichomes. *Piptocarpha rotundifolia* further differs from *P. cardenasii* by being a tree with cordiform leaves. By its shrubby vining habit and many-flowered capitula, *P. cardenasii* is somewhat similar to the five species of the third series, *Piptocarpha* subg. *Piptocarpha* sect. *Piptocarpha* ser. *Opacae* G. Lom. Sm., but each differs from *P. cardenasii* by their matted-lepidote or matted-pubescent abaxial leaf blade surfaces.

By its pointed, sclerified anther tails (Figs. 2B, 3A), shrubby habit with vining branches, concolorous leaves with loose, non-interwoven stellate abaxial blade indument (Fig. 4), and large, paleate, pluriflorous capitula in 2–13-capitulate groups per node (Figs. 5A, 6–7), *Piptocarpha cardenasii* matches formerly monotypic *Piptocarpha* subg. *Piptocarpha* sect. *Piptocarpha* ser. *Asterotrichiae* G. Lom. Sm. (the fourth of four series that Smith & Coile 2007 recognized in sect. *Piptocarpha*), where without hesitation we place the new species. Gleason (1932: 371) described *P. insignis* Gleason, a synonym of *P. asterotrichia*, as having "flowers subtended by linear-acuminate scales" (i.e., paleate), and Pruski (2013) in Flora Mesoamericana noted that the paleate condition is on

occasion found in *Piptocarpha*. *Piptocarpha* ser. *Asterotrichiae*, however, appears to be the only consistently paleate-capitulate group of *Piptocarpha*. *Piptocarpha cardenasii* thus becomes only the second recognized species of *Piptocarpha* ser. *Asterotrichiae* and its sole Colombian member. *Piptocarpha cardenasii* (Figs. 5A, 6) is distinguished from *P. asterotrichia* (Figs. 5B, 9; the protologue figure as drawn is too discolorous-leaved) by its obovate leaf blades with obtuse to rounded apices, open capitulescences with mostly pedunculate capitula, and ecostate phyllaries pubescent in a distal patch (Fig. 7). A key distinguishing *Piptocarpha cardenasii* and Peruvian-centered *P. asterotrichia* is given below.
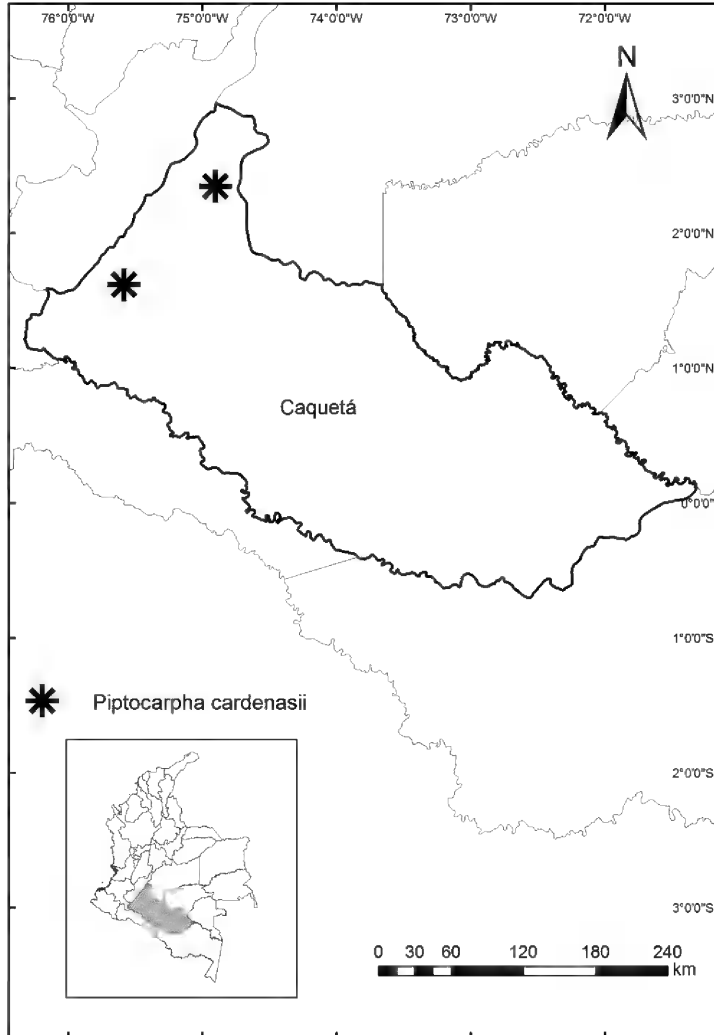
Figure 8. Distribution of *Piptocarpha cardenasii*; the coordinates of *Correa 7052* are estimated.

Figure 9. Fruiting collection of *Piptocarpha asterotrichia* showing axillary glomerules of sessile capitula with involucres constricted apically. (Topotype: Peru. Tocache, *Rios, Mori, Ortiz, Pruski & Torres 4099*).

The following key modifies couplet 5B of the subgeneric key in Smith and Coile (2007: 31). We place *Piptocarpha cardenasii* following *P. asterotrichia* in the Smith and Coile monograph, treating it as species 10.1, and in doing so we expand the limits of paleate *Piptocarpha* subg. *Piptocarpha* sect. *Piptocarpha* ser. *Asterotrichiae* to house this second species.

5B'. Capitulescences of sessile capitula in few-capitulate glomerules along main stem or along short, leafy lateral branchlets; leaf blades lanceolate, elliptic, or ovate, apices (obtuse-)acute to acuminate; phyllaries often strongly costate-apiculate ("pungently acuminate" fide Gleason 1932: 371), commonly loosely and evenly pubescent, rarely pubescent only in distal patch; (Peru, Bolivia, Ecuador, and western Brazil). .... **Piptocarpha asterotrichia** (Poepp.) Baker

5B". Capitulescences of usually pedunculate capitula in loose, open cymes mostly terminating branches, sometimes in leaf axils from the distal-most few nodes; leaf blades obovate, apices obtuse to rounded; phyllaries never strongly costate-apiculate, densely pubescent only in an elongate distal patch; (western Amazonian Colombia). .... **Piptocarpha cardenasii** Pruski

The broad-tipped pappus bristles further distinguish *Piptocarpha cardenasii*. The moderately short stellate-trichome stipes and the tendency towards terminal capitulescences in the three specimens of *P. cardenasii* in front of us may prove to be distinguishing characters once more material of the new species becomes available for study. *Piptocarpha cardenasii* does not particularly resemble any of the nine previously described Colombian species of *Piptocarpha* (5 of them described by Cuatrecasas 1955) (see Appendix 1).

ACKNOWLEDGEMENTS

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APPENDIX 1: Infrageneric placements (adapted from Smith & Coile 2007) and distributions of the ten Colombian species of *Piptocarpha*.

Piptocarpha subg. **Hypericoides** (Sch. Bip.) G. Lom. Sm. (no species reported in Colombia).
Piptocarpha subg. **Piptocarpha** (2 sections, 2 series, and 10 species in Colombia).
Piptocarpha subg. **Piptocarpha** sect. **Piptocarpha**   (capitula mostly 7–22-flowered; 2 series and 2 species in Colombia).
Piptocarpha subg. **Piptocarpha** sect. **Piptocarpha** ser. **Asterotrichiae** G. Lom. Sm.   (1 species; abaxial leaf surface trichomes loose, not interwoven).
1. *Piptocarpha cardenasii* Pruski (endemic to Amazonian Colombia).
[provisionally excluded from Colombia: *P. asterotrichia*, the citation by Robinson (1999: 77) of this species in Colombia is not vouchered; Smith and Coile (2007) cited *P. asterotrichia* in Peru and Bolivia; also Brazil (*Daly et al. 10957,* MO, NY, US) and Ecuador (*Freire & Santi 3235*, MO, US)].
Piptocarpha subg. **Piptocarpha** sect. **Piptocarpha** ser. **Opacae** G. Lom. Sm.   (1 species; abaxial leaf surface trichomes matted and interwoven).
2. *Piptocarpha opaca* (Benth.) Baker (widespread in northern South America; represented in Colombia by *P. opaca* subsp. *piraparanaensis* G. Lom. Sm.)**.**
[excluded from Colombia: *P. polycephala* Baker, the erroneous report of this eastern Guayana Highland species by Bernal et al. (2015: 888) was based on *Croat 54238* from Bolívar, Venezuela].
Piptocarpha subg. **Piptocarpha** sect. **Oocephalus** (Sch. Bip.) G. Lom. Sm.   (capitula 1–6-flowered; 8 species in Colombia).
3. *Piptocarpha atratoensis* Cuatr. (endemic to Choco, Colombia).
4. *Piptocarpha boyacensis* Cuatr. (endemic to Boyacá, Colombia).
5. *Piptocarpha foliosa* Cuatr. (Amazonian Brazil, Colombia, and Peru).
6. *Piptocarpha gutierrezii* Cuatr. (Colombia, Venezuela, Ecuador, Peru).
7. *Piptocarpha jonesiana* G. Lom. Sm. (endemic to Amazonian Colombia).
8. *Piptocarpha poeppigiana* (DC.) Baker (widespread, South America to Mexico).
9. *Piptocarpha richteri* Cuatr. (endemic to Putumayo, Colombia).
10. *Piptocarpha triflora* (Aubl.) Benn. ex Baker (widespread in northern South America).

NEW COMBINATIONS
IN *PSEUDOCYMOPTERUS* AND *CYMOPTERUS* (APIACEAE)

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ABSTRACT

Molecular and morphological phylogenetic analyses indicate that many of the perennial endemic genera of North American Apiaceae subfamily Apioideae are either polyphyletic or nested within paraphyletic groups. In light of these results, taxonomic changes are needed to ensure that ongoing efforts to prepare state, regional, and continental floristic treatments of Apiaceae reflect recent findings. Thus, we make two new combinations in *Pseudocymopterus* and one in *Cymopterus*: **Pseudocymopterus beckii** (Welsh & Goodrich) S.R. Downie, **comb. nov.**, **Pseudocymopterus macdougalii** (Coult. & Rose) J.F. Smith, S.R. Downie & Mansfield, **comb. nov.**, and **Cymopterus glomeratus** (Nutt.) DC. var. **parvus** (Goodrich) Mansfield & K.M. Mason, **comb. nov.**

The Perennial Endemic North American (PENA) clade of Apiaceae is a monophyletic group of 21 genera (~200 taxa) (Downie et al. 2010; Nesom 2012; Hartman and Nesom 2012). Many of these genera, such as *Cymopterus*, *Lomatium*, *Tauschia*, and *Pseudocymopterus*, have their center of diversity in the western USA and this clade as a whole represents one of the largest endemic plant radiations in North America. The PENA clade has been the focus of recent molecular studies that have shown the artificiality of many of its genera, as 10 are polyphyletic or paraphyletic and another 6 are nested within paraphyletic groups (Downie et al. 2002; Sun & Downie 2004; Sun et al. 2004, 2010a, 2010b; Feist et al. 2013; George et al. 2014). Although additional studies are needed before a well-resolved phylogenetic hypothesis of the entire PENA clade is completed, regional and continental level floristic works (such as the treatment of Apiaceae, vol. 13, for Flora of North America) are proceeding and nomenclatural changes need to be made for those species that have strong molecular phylogenetic support placing them in another genus (see also Feist et al. 2017). In some cases, future phylogenetic analyses may result in further name changes, but the nomenclatural changes proposed here represent our best current understanding of the phylogeny and morphology of these plants and are necessary to improve the utility of forthcoming works. Thus, we make two new combinations in *Pseudocymopterus* and one in *Cymopterus*.

Pseudocymopterus beckii (Welsh & Goodrich) S.R. Downie, **comb. nov.** *Cymopterus beckii* Welsh & Goodrich, Brittonia 33: 297, Fig. 4. 1981.

Phylogenetic analyses of molecular data (Sun et al. 2004; Sun & Downie 2004, 2010a) and combined morphological and molecular data (Sun & Downie 2010b) place this taxon unambiguously in the same clade as *Pseudocymopterus montanus* (A. Gray) Coult. & Rose, the type species for the genus *Pseudocymopterus*, and away from the type species of *Cymopterus* and its allies. The results of recent phylogenetic analyses of additional plastid and nuclear markers corroborate this placement (Feist et al. 2013). Cronquist (1997) suggested previously that *P. montanus* and *C. beckii* might be conspecific. We therefore propose this new combination.

Pseudocymopterus macdougalii (Coult. & Rose) J.F. Smith, S.R. Downie & Mansfield, **comb. nov.** *Aletes macdougalii* Coult. & Rose, Contr. U.S. Natl. Herb. 7: 107. 1900; *Cymopterus macdougalii* (Coult. & Rose) Tidestr.; *Oreoxis macdougalii* (Coult. & Rose) Rydb.

Phylogenetic analyses of molecular data (Sun et al. 2004; Sun & Downie 2004, 2010a; George et al. 2014) and combined morphological and molecular data (Sun & Downie 2010b) place this taxon unambiguously in the same clade as *Pseudocymopterus montanus*, the type species for the

genus *Pseudocymopterus*, and the aforementioned new combination *P. beckii*. We therefore propose this new combination.

Cymopterus glomeratus (Nutt.) DC. var. **parvus** (Goodrich) Mansfield & K.M. Mason, **comb. nov.**
    Cymopterus acaulis (Pursh) Raf. var. *parvus* Goodrich, Great Basin Nat. 46: 79. 1986.

    Five varieties have been long recognized under *Cymopterus acaulis*: vars. *acaulis, fendleri, greeleyorum, higginsii,* and *parvus*. On the basis of multivariate analysis of variance and principal component analysis of 288 specimens representing the known morphological variability and geographic distribution of the species, Sun et al. (2005) proposed that plants in this complex be recognized as one morphologically variable species, *C. glomeratus*, with no varieties. At that time the name *C. glomeratus* was used to replace the widely used but illegitimate name *C. acaulis* (Sun et al. 2005). Phylogenetic analysis of molecular data (Sun et al. 2004; Sun & Downie 2004, 2010a) and combined morphological and molecular data (Sun & Downie 2010b) supported *C. glomeratus* as monophyletic, with the addition of *Lomatium concinnum* (Osterh.) Mathias and possibly *C. newberryi* (S. Wats.) M.E. Jones. The molecular study of George et al. (2014) corroborated the placement of *L. concinnum* within a strongly supported and monophyletic *C. glomeratus*, treating it as *C. glomeratus* var. *concinnus* (Osterh.) R.L. Hartm. George et al. (2014) also made the new combination *C. glomeratus* var. *greeleyorus* R.L. Hartm. by sampling four accessions that resolved as a monophyletic infraspecific taxon within the C. *glomeratus* clade. They also substantiated the combination of *C. glomeratus* var. *fendleri* (A. Gray) R.L. Hartm. (Hartman 2006) by recovering the two sampled accessions as monophyletic within *C. glomeratus*.

    Despite the morphological overlap of all varieties of *Cymopterus glomeratus*, except var. *concinnus* (Sun et al. 2005), the recognition of varieties within *C. glomeratus* (Hartman 2006; George et al. 2014) allows new floristic works (such as the treatment of Apiaceae, vol. 13, for Flora of North America) to treat infraspecific taxa under *C. glomeratus*. Though no evidence presented since 2005 pertains to C. *glomeratus* var. *parvus* (George et al. 2014 did not sample these taxa), this variety has been recognized under *C. acaulis*. We propose here a new combination to allow floristic authors the opportunity to recognize the formerly recognized variety of *C. acaulis* in a legitimate combination — *Cymopterus glomeratus* var. *parvus*. *Cymopterus glomeratus* var. *parvus* is a local endemic variety in western Utah.

    We do not, however, make a new combination for *Cymopterus acaulis* (Pursh) Raf. var. *higginsii* (S.L. Welsh) Goodrich; rather this name is placed in synonymy under *C. glomeratus* var. *fendleri* (A. Gray) R.L. Hartm. We are in agreement with Cronquist (1997), who equated *C. acaulis* var. *higginsii* with *C. acaulis* var. *fendleri*.

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SEYMERIA ANITA (OROBANCHACEAE), UNA NUEVA ESPECIE DEL ESTADO DE QUERÉTARO, MÉXICO

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ABSTRACT

Seymeria anita from the state of Querétaro, México, is described and illustrated. These plants have a woody base as well as completely glandular-pubescent leaves and stems. Leaves are up to 1.7 cm long and up to 0.8 cm wide. The capsules are densely glandular-stipitate, on pedicels 0.6–0.8 cm long. The plants grow at 800-2100 m elevation.

RESUMEN

Se describe e ilustra como especie nueva a *Seymeria anita* del estado de Querétaro, México. Son plantas que tienen tallos leñosos en su base y hojas completamente glandular-pubescentes. Las cuales tienen hasta 1.7 cm de largo y 0.8 cm de ancho. Cápsulas densamente estipitado-glandulares, pedicelos de 0.6 a 0.8 cm de largo. Estas plantas prosperan a 800-2100 m de elevación.

El género *Seymeria* Pursh (1814) contiene hierbas anuales y perennes que se distribuyen del sureste de Estados Unidos al sur de México. En este último, se presenta casi a todo lo largo de su territorio, donde un buen número de sus taxones se conocen sólo de la localidad tipo o de áreas muy restringidas. Pennell (1925) reconoció 22 especies, que fueron tratadas dentro del género *Afzelia* (Gmelin 1791); Billie L. Turner (1982, 1995) publicó revisiones del grupo, en las que considera a *Seymeria* con 15 especies en México. Sin embargo, en la revisión del género para la Flora del Bajío se destaca la necesidad de hacer más trabajo para lograr conocer mejor este grupo en este país.

Turner en sus trabajos de las décadas pasadas señaló la necesidad de un mejor entendimiento del género para el territorio nacional. En este trabajo la observación de muchos especímenes de herbarios mexicanos, muestra una notable carencia de colectas para el país; la mayoría de las cuales provienen del centro y del norte, donde se ha puesto la mayor atención para colectar, por lo que se deduce la falta de exploraciones a lo largo y ancho de su geografía. Por lo tanto se recomienda hacer una revisión del grupo, incluyendo en la exploración el sur y el oeste, así como la porción sur de los Estados Unidos.

El género *Seymeria* ha sido estudiado por varios autores durante mucho tiempo. Uno de los últimos, Turner (1982) al revisar los taxa mexicanos menciona que hay en total 12, reduciendo a sinonimia 10 nombres y describiendo tres especies nuevas: *S. falcata*, *S. pennellii*, and *S. tamaulipana* (Turner 1982). Este mismo autor en 1995 propuso *S. cualana*, *S. gypsophylla*, y *S. pailana* también como nuevas, llevando el número total a 15.

En este grupo existe un fuerte sobrelapamiento en ciertos caracteres, por ejemplo en la densidad de la pubescencia y en la forma de las hojas. Lo cual en muchas ocasiones hace difícil la determinación confiable de los especímenes. Igualmente, las condiciones ecológicas donde estas plantas prosperan son muy heterogéneas.

Por otra parte, durante la colecta de plantas para preparar La Flora del Bajío en años recientes, se colectaron algunos especímenes en el norte del estado de Querétaro que pertenecen a un nuevo taxon. Por lo que a continuación se propone la descripción como especie nueva de *S. anita*:

SEYMERIA ANITA E. Carranza y C. Medina, **sp. nov.** Figure 1. **TIPO: MEXICO. Querétaro.** Municipio de Jalpan, El Guayabo, 5-6 km al NE de Rancho Nuevo, altitud 750 msnm, 16 Nov 1991, laderas con bosque de encino *L. López 196* (holotype IEB!).

Herba perennis 40–90 cm alta; caules sparse ad dense glanduloso-pubescentes; folia plerumque sessilia lanceolata indivisa vel interdum lobata 3–10(17) mm longa, 1.4(8) mm lata, ad basem cuneata, ad apicem obtusa ad rotundata, ad marginem integra ad crenati-dentata, glanduloso-pubescens; flores solitarii axillares, pedicellis (5)8–12(15) mm longis glanduloso-pubescentibus; calyx segmentis 1–2(3.5) mm longis, glandulis sessilibus vel breviter stipitatis tectis; corolla lutea 7.5–10 mm longa, tubo 2.5–5 mm longo, lobulis 2.5–5 mm longi, 2.5–4 mm lati, extus glabra, intus cum pilis in annulo dispositis; stamina filamentis 1.5–2 mm longis ad marginem pilosis, antheris lanceolatis ca. 2 mm longis; stylus 4–5 mm longus, stigmate capitato piloso; capsula ovoidea 6–8 mm longa dense glanduloso-pubescens; semina 1–1.5 mm longa, brunnea.

Hierba perenne, erecta, de 40 a 90 cm de alto; tallos esparcida a densamente pubescentes, con pelos glandulares cortamente estipitados; hojas sésiles o en ocasiones parecen ser cortamente pecioladas, simples, lámina angosta a anchamente lanceolada, a en ocasiones lobada, a veces deflexa, de 3–10(17) mm de largo, de 1–4(8) mm de ancho, base cuneada a decurrente, ápice obtuso a redondeado, margen entero a crenado-dentado, uninervadas, con la vena prominente en el envés, la pubescencia glandular cortamente estipitada; flores solitarias, amarillas, axilares, a veces deflexas; pedicelos de (5)8–12(15) mm de largo, rectos a curvados, glandular-pilosos; cáliz de 2–5 mm de largo, campanulado, sépalos 5, de 1–2(3.5) mm de largo, lanceolados a triangulares, extendidos o curvados, ápice agudo a redondeado, enteros, con glándulas sésiles o cortamente estipitadas; corola amarilla, campanulada, ligeramente recurvada, de 7.5–10 mm de largo, tubo de 2.5–5 mm de largo, lóbulos de 2.5–5 mm de largo por 2.5–4 mm de ancho, la superficie externa glabra y brillante, la interna ocasionalmente con algunos pelos glandulares, con un anillo denso de pelos en la unión de los filamentos que se extiende hasta la base posterior de los lóbulos, margen ciliado; estambres de 2–4 mm de largo, filamentos de 1.5–2 mm de largo, densamente pilosos en los márgenes; anteras lanceoladas de aproximadamente 2 mm de largo, de color marrón oscuro en el centro, la sutura amarillo-oscuro, casi tan largo como la antera; estilo ± filiforme, de 4–5 mm de largo, glabro; estigma capitado, piloso; cápsula ovoidea, de 6–8 mm de largo, densamente estipitado-glandular; semillas numerosas, circulares, redondeadas, ovoides o iregulares, de 1–1.5 mm de largo, de 1 mm de ancho, la testa algo alada-segmentada y reticulada, de color ligeramente café.

Material adicional revisado. MEXICO. Querétaro. Municipio de Jalpan, La Guerra, 3-4 km al oriente de Carrizal de los Durán, 17 Dic 1991, *Servín 1475* (IEB); 8 km al NW de Rancho Nuevo, camino al río Santa María, 6 Dic 1989, *Rubio 1381* (IEB); Municipio de Pinal de Amoles, 1.5 km al S de San Pedro Escanela, 3 Oct 1991, *Carranza 3594* (IEB); Municipio de San Joaquín, brecha San Joaquín-El Durazno, 18 Nov 1998, *Hernández 11754* (IEB).

Seymeria anita es una planta robusta que llega hasta 80-90 cm de altura, con la base algo leñosa. Se parece a *S. integrifolia* Greenm. en sus hojas simples y ocasionalmente lobadas, así como en el tamaño y la pubescencia interna de la corola, pero difiere de ella en la pubescencia de sus tallos, esparcidamente puberulentos y con escasas glándulas sésiles, mientras que en la nueva especie la pubescencia es moderada a densa y los pelos son glandulares. También difiere en el tamaño, forma y pubescencia del cáliz; los sépalos en *S. integrifolia* son lineares y glabros, de 3 a 3.5 mm de largo y en *S. anita* son lanceolados a triangulares, glandulares, de 1 a 3.5 mm de largo.
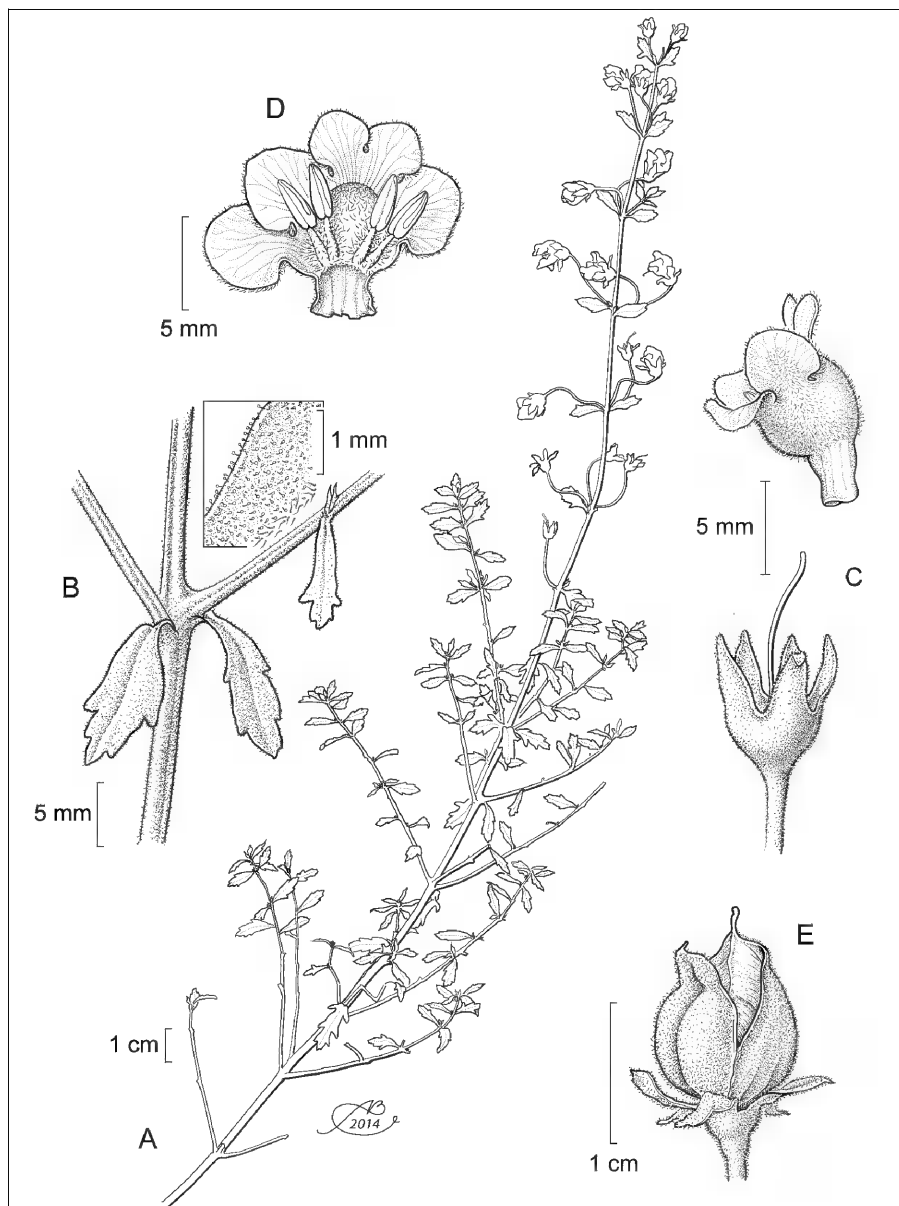
Figura 1. *Seymeria anita*. A. Rama, mostrando flores y hojas. B. Hojas y ramas. C. Cáliz y pistilo. D. Flor interna. E. Fruto.

Seymeria integrifolia crece principalmente en Jalisco y Nayarit, mientras que *S. anita* solo se conoce de Querétaro, donde también se ha encontrado a *S. decurva* Benth. y a *S. virgata* (Kunth) Benth. La diferencia más conspicua con la primera se presenta en sus estambres más largos y en la corola más grande, mientras que de *S. virgata* difiere en las láminas foliares bipinnatifidas en ésta y no divididas en la nueva especie.

Estas plantas se han encontrado en el noreste de Querétaro cerca con el límite del estado de San Luis Potosí, sobre laderas de la Sierra Gorda aledañas al Río Santa María así como al este y sureste de Pinal de Amoles.

Las poblaciones encontradas se ubican entre 750 y 2100 msnm, en encinares bajos y ocasionalmente entre algunos pinos. Otras especies frecuentes con las que generalmente se asocia conformando los encinares, son *Quercus polymorpha*, *Pinus greggii*, *Arbutus xalapensis*, y *Rhus trilobata*; y en sitios de mayor humedad también se pueden presentar *Liquidambar styraciflua* y *Quercus* spp. Por lo regular las plantas de esta nueva especie florecen de octubre a diciembre.

El epíteto dado se nombra en honor de Ana Rzedowski Calderón, hija de los Drs. Jerzy Rzedowski y Graciela Calderón de Rzedowski. Que en incontables ocasiones acompañó a sus padres durante el trabajo de campo y que frecuentemente consistió en largas caminatas. Que esta dedicatoria valga como un homenaje a sus esfuerzos.

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COMPOSITAE OF CENTRAL AMERICA–IX.
TALAMANCASTER (ASTEREAE), A NEW GRANGEOID GENUS FROM GUATEMALA, COSTA RICA, PANAMA, AND VENEZUELA

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ABSTRACT
The new grangeoid genus **Talamancaster** Pruski, **gen. nov.** (Compositae: Astereae), is described and includes six páramo-centered species. *Talamancaster* is known only from Guatemala, Costa Rica, Panama, and Venezuela, but should be looked for in Mexico and Colombia. *Talamancaster* is distinguished by its short, pinkish rays in few series, bisexual 5-merous disk florets with glabrous corollas and apiculate anthers, and epappose, compressed cypselae. The six component species are small herbs, either subscapose or with few-leaved stems, and were described in *Lagenophora*, then transferred to *Myriactis* (both Lagenophorinae). *Talamancaster* differs from circumaustral scapose *Lagenophora* by bisexual (vs. functionally staminate) disk florets with campanulate (vs. funnelform), glabrous (vs. papillose-glandular) corollas, and from leafy stemmed *Myriactis* by 5-merous (vs. 4-merous) disk florets with glabrous (vs. papillose-glandular) corollas. Phylogenetic study by Noyes and Rieseberg and Nakamura et al. (coupled Nesom's with subtribal classification) are neither complete nor fully resolved, but nevertheless recovered *Lagenophora* (*Talamancaster*) *panamensis* as sister to *Laennecia* Cass. (Podocominae) rather than to *Myriactis* (Lagenophorinae). *Talamancaster*, however, matches no genera of either subtribe (or of tribe Astereae) and is described as a new genus, albeit unplaced subtribally. Six new combinations are proposed: **Talamancaster andinus** (V.M. Badillo) Pruski, **comb. nov.**, **T. cuchumatanicus** (Beaman & De Jong) Pruski, **comb. nov.**, **T. minusculus** (Cuatr.) Pruski, **comb. nov.**, **T. panamensis** (S.F. Blake) Pruski, **comb. nov.**, **T. sakiranus** (Cuatr.) Pruski, **comb. nov.**, and **T. westonii** Cuatr.) Pruski, **comb. nov.** SEM micrographs of cypselae in *Laestadia*, *Lagenophora, Myriactis*, *Podocoma*, and *Talamancaster* are provided, as are figures that illustrate key differences in habit and flowers.

The new genus *Talamancaster* Pruski (Compositae: Astereae) is described and includes six neotropical species. The species are short-radiate, small, subscapose herbs with pauciseriate pistillate florets usually with pinkish corollas, bisexual 5-merous disk florets with glabrous corollas and apiculate anthers, and cypselae that are epappose, compressed, glandular-substrate, and prominently costate marginally (viz Figs. 1, 11–14). Each of the six species of *Talamancaster*, by their epappose glandular-substrate flat-cypselae, was described in Patagonian and New Zealand-centered *Lagenophora* Cass. (conserved in spelling over the orthographic variant *Lagenifera*). The earliest described species, *L. panamensis* (now *T. panamensis*), was noted by Blake (1939) to resemble *L. maviensis* H. Mann, treated by Nesom (2001) as *Keysseria maviensis* (H. Mann) Cabrera within *Keysseria* sect. *Sandwicactis* Nesom. Indeed, *K. maviensis* is similar in its glabrous disk corollas, but *Keysseria* differs from *Talamancaster* by being a thick-leaved, moderately stout perennial with deltate anther appendages composed of bullous cells, and by having 4-merous disk corollas.

Cabrera (1966) revised *Lagenophora*, recognizing 15 species and placing 12 of them in scapose *Lagenophora* sect. *Lagenophora,* which contained the type element from Patagonia as well as the Old World species. In a review of *Lagenophora* in New Zealand, Drury (1974) noted that Cabrera (1966) "following the lead of Beaman & De Jong (1965)" placed the three then-described neotropical species (*L. andina* V.M. Badillo 1947, *L. cuchumatanica* Beaman & De Jong 1965, and *L.*

panamensis S.F. Blake 1939) in the newly described subscapose *Lagenophora* sect. *Pseudomyriactis* Cabrera (1966). Drury also noted that the glabrous disk corollas of sect. *Pseudomyriactis* Cabrera serve to set it apart from section *Lagenophora*. Subsequently, Cuatrecasas (1982) described three further species in *Lagenophora* sect. *Pseudomyriactis*: *L. minuscula* Cuatr., *L. sakirana* Cuatr., and *L. westonii* Cuatr., each endemic to the Talamanca Mountains in southeastern Costa Rica and western Panama. Vélez (1981) and Cuatrecasas (1986) transferred all six species of *Lagenophora* sect. *Pseudomyriactis* to Asia- and Malaysia-centered leafy-stemmed *Myriactis*. Placement of these species in either *Lagenophora* or *Myriactis* is supported by roughly similarly compressed cypselae.

Morphologically, however, notwithstanding the moderately flattened cypselae, *Talamancaster* does not match either *Lagenophora* or *Myriactis*. The three genera share the characters of grangeoid genera, a group mostly characterized by herbaceous habit, 2+-seriate pistillate florets (viz Figs. 2, 7, 27), moderately herbaceous phyllaries, and obviously compressed cypselae (Fayed 1979; Nesom 1994a, 2000; Nesom & Robinson 2007; Pruski 2011). *Lagenophora* is a rosette plant with obviously rostrate cypselae and functionally staminate 5-merous disk florets with papillose-glandular, funnelform corollas (Fig. 2). *Myriactis* is a tall leafy stemmed plant, has 4-merous, bisexual disk florets with papillose-glandular, campanulate-salverform corollas, and mostly erostrate cypselae (Figs. 3–4). In herbarium material of *Myriactis* the 4-merous disk florets and their 4-lobed corollas are often discernible at a glance by their overlapping corolla lobes, two spreading to the right and two to the left.
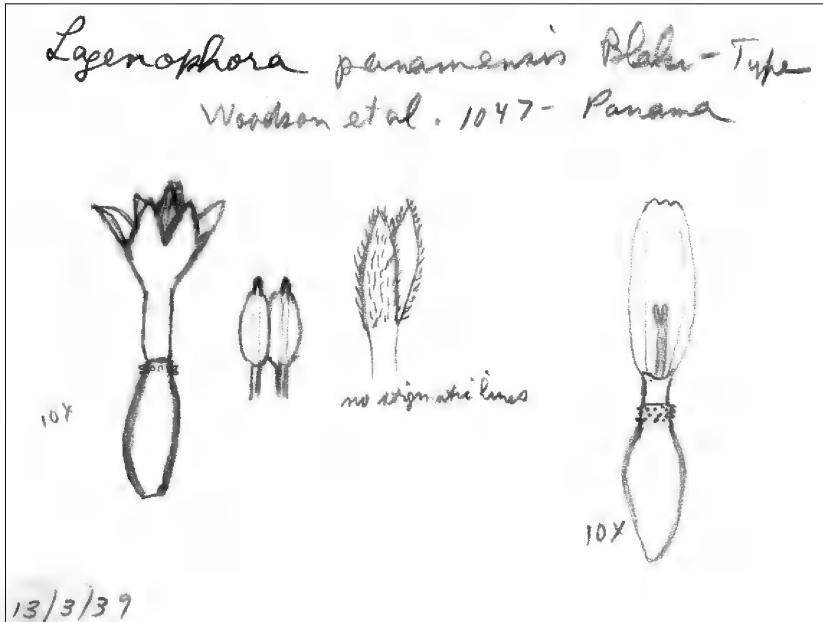
Figure 1. *Talamancaster panamensis* floral sketch by Sidney Fay Blake, clipped to holotype of *Lagenophora panamensis*. The essential generic characters drawn include apiculate anthers, the flattened glandular-necked cypselae of a ray floret and a bisexual disk floret, and the glabrous campanulate disk corolla. Cabrera (1966: 305) mistakenly characterized the disk florets of *Talamancaster panamensis* as "apparently mostly sterile," but instead the disks on the holotype set fruit. (From *Woodson et al. 1047*, US).
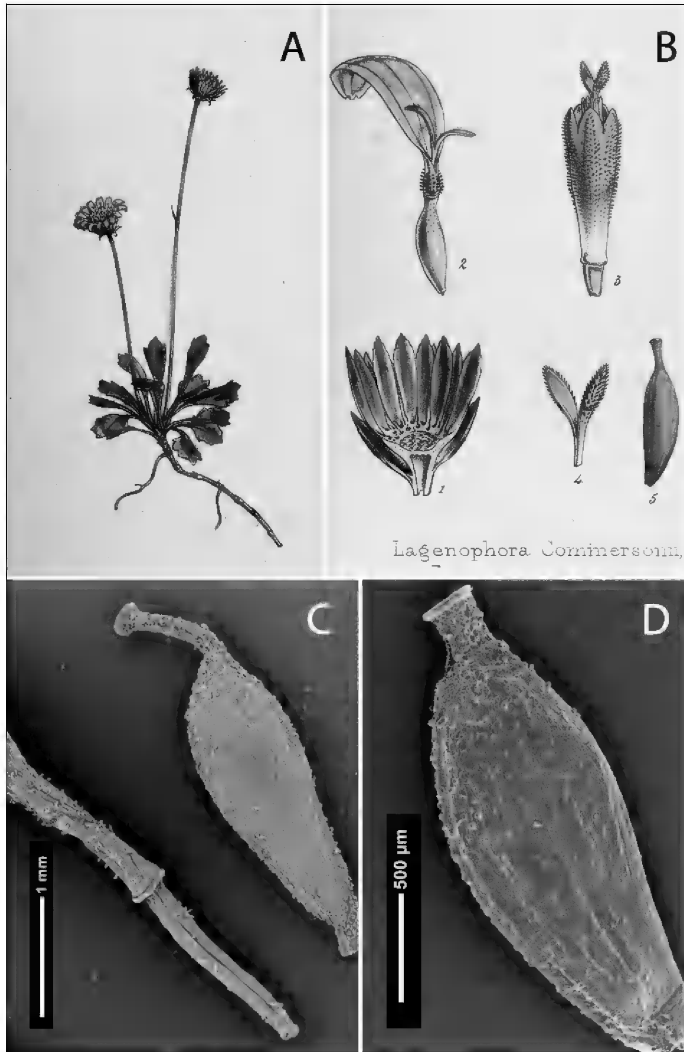
Figure 2. Diagnostic characters of *Lagenophora* (subtribe Lagenophorinae). A. Habit of *Lagenophora nudicaulis* (Lam.) Dusén. B. *Lagenophora nudicaulis* floral details, including a functionally staminate 5-merous disk floret with a funnelform, papillose-glandular corolla. C. SEM micrograph of sterile disk floret (lower left) showing papillose-glandular corolla tube and cylindrical ovary, and mature flat rostrate ray cypsela (upper right) of *Lagenophora stipitata* (Labill.) Druce. D. SEM micrograph of mature flat ray cypsela of *Lagenophora hariotii* Franch. (A–B from J.D. Hooker, Bot. Antarctic Voy., vol. 1, part 2 (i.e., Fl. Antarct.) tab. 108 left, 1846, as *Lagenophora commersonii* Wedd., which along with the generitype of *Lagenophora*, *Calendula magellanica* Willd., were given by Cabrera 1966, 1971 as synonyms of *Lagenophora nudicaulis*; C Papua New Guinea, *Croft et al. 65116*, MO; D Tierra del Fuego, *Roivainen 1643*, MO).

Figure 3. *Myriactis wightii* DC. (subtribe Lagenophorinae), showing leafy stem and the 4-merous, campanulate-salverform disk corollas. (From R. Wight, Icones plantarum Indiae Orientalis 3: tab. 1091. 1846).
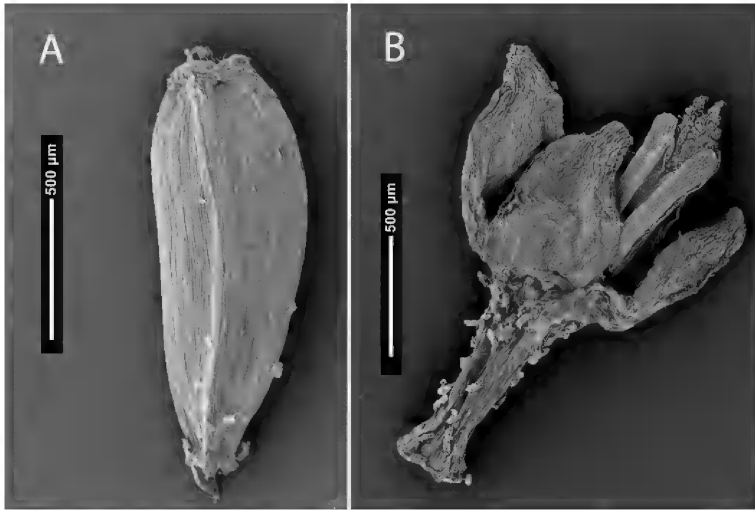
Figure 4. SEM micrographs of *Myriactis nepalensis* Less., the generitype of *Myriactis* (subtribe Lagenophorinae). A. Moderately compressed disk cypsela showing truncate apex and lateral face with a weak medial nerve. The abaxial (outer) margin of the asymmetrically curved cypsela is on the right. B. Campanulate-salverform, 4-merous disk corolla showing papillose-glandular trichomes of the tube. Some species of *Myriactis* have short-rostrate cypselae. (China, *Heng et al. 20639*, MO).
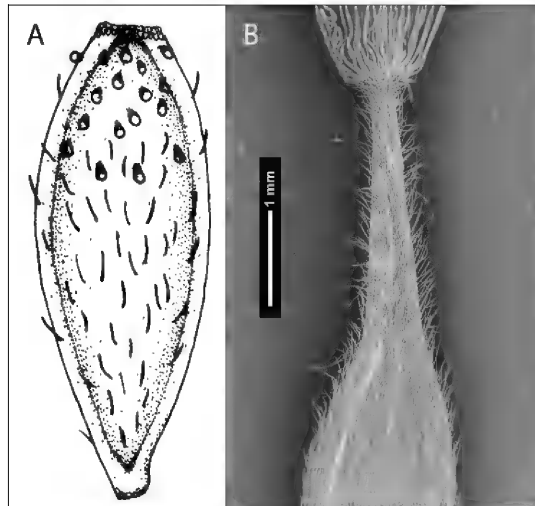
Figure 5. Thick-margined compressed cypselae of representative pappose genera of subtribe Podocominae. A. Erostrate, distally glandular cypsela of *Laennecia araneosa* (Urb.) G. Sancho & Pruski, pappus bristles removed. B. SEM micrograph of rostrate, pappose cypsela of *Podocoma hieraciifolia* (Poir.) Cass. (A Dominican Republic, *Ekman 13566*, US, reproduced from Sancho & Pruski 2004; B Paraguay, *Zardini & Vera 48287*, MO).
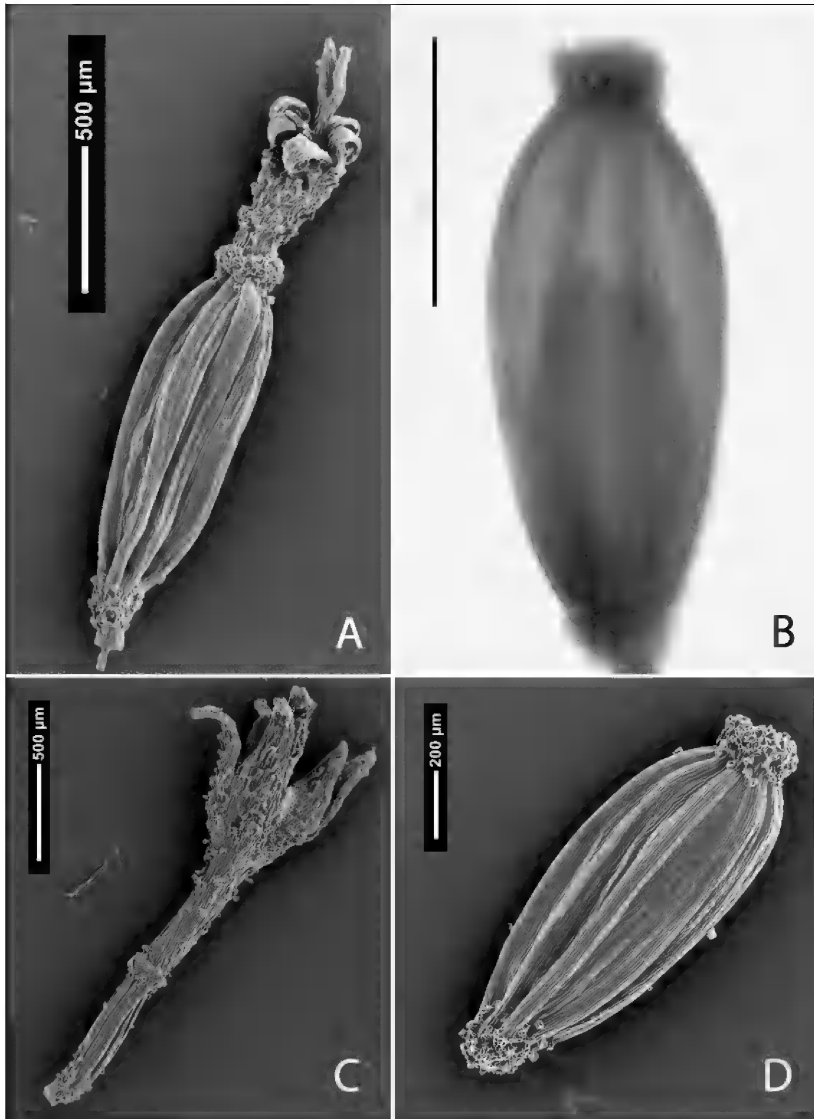
Figure 6. Terete cypselae of *Laestadia costaricensis* (subtribe Hinterhuberinae). A. Pistillate marginal floret with narrowly campanulate corolla and maturing fruit. B. Five-ribbed ovary of marginal floret showing erect basal ovule. C. Functionally staminate disk floret with cylindrical sterile ovary and broadly campanulate corolla. D. Mature pluricostate cypsela of marginal floret. The voucher for this figure is from Cerro Chirripó (Suessenguth 1942 noted the species there), where three of the six *Talamancaster* species occur. (Costa Rica, *Pruski et al. 3948*, MO). [A, C–D are SEM micrographs; scale bar in B 0.8 mm].

Figure 7. Capitulum of *Talamancaster andinus*, showing the many pauciseriate pink rays and fewer disk florets. (*Pruski et al. 3935*).

Figure 8. Unusually robust individual of *Talamancaster andinus*, showing stems few-branched distally. (*Pruski et al. 3935*).
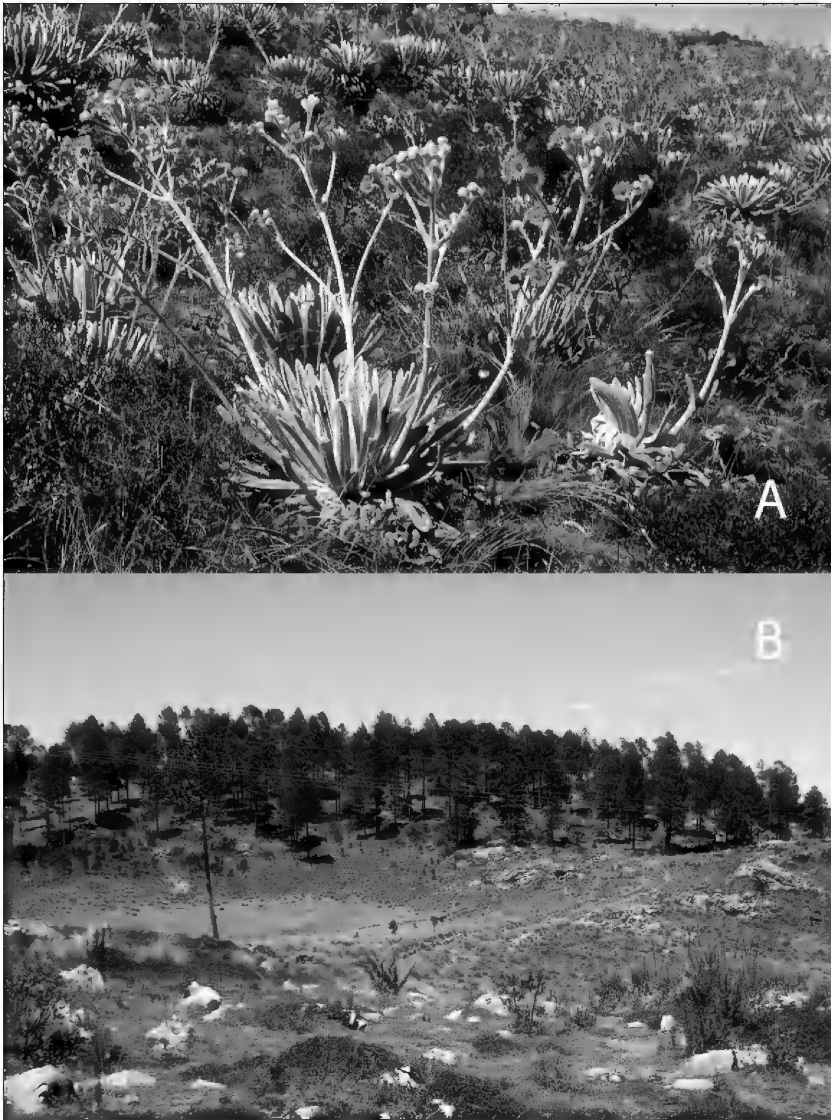
Figure 9. Two extra-Talamancan habitats of species of *Talamancaster*. A. The type locality of *Talamancaster andinus* in páramo near Laguna de Mucubají, Venezuela, showing yellow-rayed caulirosulate *Espeletia schultzii* Wedd. (*Pruski et al. 1346*). B. Type locality of *Talamancaster cuchumatanicus* near *Pinus* grove in the Sierra de los Cuchumatanes, Guatemala. This locality is near Todos Santos Cuchumatán, which sits in the glacier-carved U-shaped Río Limón valley. *Talamancaster cuchumatanicus* is found also in pine forests on the Tecúm Uman Ridge. Neither *Pinus* nor *Espeletia* is native to Costa Rica or Panama.

Table 1. Select characters of *Lagenophora*, *Talamancaster*, and *Myriactis*.

LAGENOPHORA	TALAMANCASTER	MYRIACTIS
Basically circumaustral, slightly extending into Malaysia and SE Asia.	Guatemala, Costa Rica, Panama, and Venezuela.	Asia- and Malaysia-centered.
Scapose.	Subscapose or leafy stemmed.	Leafy stemmed.
Disk florets functionally staminate.	Disk florets bisexual.	Disk florets bisexual.
Disk corollas 5-lobed, funnelform, papillose-glandular.	Disk corollas 5-lobed, campanulate, glabrous.	Disk corollas 4-lobed, campanulate-salverform, papillose-glandular.
Cypselae rostrate.	Ray cypselae and usually disk cypselae collared (disk cypselae of *T. minusculus* and *T. sakiranus* without collar).	Cypselae erostrate and flat on top (generitype) to other species short-rostrate or collared.
Disk ovaries terete, never forming fruit, obviously much shorter than ray cypselae.	Disk cypselae compressed, sometimes midnerve visible, thick-margined, similar to rays, when not pollinated ovary nearly as long as ray cypselae.	Disk cypselae compressed, sometimes weakly 4-ribbed, sometimes slightly dissimilar to those of rays.

Talamancaster, on the other hand, is distinguished from both by being a small leafy- or bracteate-stemmed herb, by having bisexual, 5-merous disk-florets with glabrous, campanulate corollas, and by ray (and often disk) cypselae with a densely viscid-glandular collar. Table I summarizes the differences between *Lagenophora*, *Myriactis*, and *Talamancaster* and updates Hind (2004), where a larger table distinguishing the core genera (viz Nesom 2001) of the *Lagenophora* group was given. As mentioned by Drury (1974), *Talamancaster* as a distinct lineage was first noted by Beaman and De Jong (1965), who said "the Central and northern South American species seem to have more characters in common among themselves than with the other members of *Lagenophora*."

While *Talamancaster* is distinct from *Lagenophora* and *Myriactis*, by morphology *Talamancaster* nevertheless seems similar to them, as well as to the remaining core genera of the *Lagenophora* group. *Talamancaster* is also moderately similar to terete-fruited *Laestadia* (subtribe Hinterhuberinae; viz Fig. 6). Phylogenetic studies by Noyes and Rieseberg (1999) and Nakamura et al. (2012), although neither complete nor fully resolved, coupled with Nesom's subtribal classification (Nesom 1994a; Nesom & Robinson 2007) recover *Lagenophora* (*Talamancaster*) *panamensis* as sister to *Laennecia* Cass. (Podocominae) rather than to *Myriactis* (Lagenophorinae) or *Laestadia* (Hinterhuberinae). Noyes and Rieseberg (1999) said *Lagenophora* (*Talamancaster*) *panamensis* is close "to the base of the North American clade, supporting a possible South American origin for North American Astereae." Nakamura et al. (2012) found *Lagenophora* to be monophyletic. Jafari et al. (2015) noted *Myriactis* is monophyletic, based on *Myriactis wallichii* Less. (their sequence data) recovered as sister to *Myriactis humilis* Merr. (as sampled by Noyes & Rieseberg 1999). *Myriactis* as

circumscribed here is excluded from the Americas and no longer should be used as an example of an amphitropically distributed genus.

The phylogenies suggest that *Talamancaster* should not be positioned in Lagenophorinae, but morphologically *Talamancaster* matches neither Hinterhuberinae nor Podocominae. All Hinterhuberinae are terete-fruited and all Podocominae are pappose (viz Nesom 1994a, 1994b; Nesom & Robinson 2007; Sancho & Karaman-Castro 2008; Karaman-Castro & Urbatsch 2009; Sancho et al. 2010), thus flat-fruited epappose *Talamancaster* is at odds with both. In any event, *Talamancaster* matches no genus of tribe Astereae, and although unplaced subtribally, it is described here as a new genus. *Talamancaster* is named in advance of its appearance in *Flora Mesoamerica*, where its type is intentionally not stated, albeit given as heterotypic from *Lagenophora* sect. *Pseudomyriactis*.

TALAMANCASTER Pruski, **gen. nov.** **TYPE:** *Lagenophora westonii* Cuatr. [≡ *Talamancaster westonii* Cuatr.) Pruski].

Lagenophora sect. *Pseudomyriactis* Cabrera, Blumea 16: 303. 1966. **TYPE:** *Lagenophora panamensis* S.F. Blake [≡ *Talamancaster panamensis* (S.F. Blake) Pruski].

Herbae perennes humiles rhizomatosae, foliis radicalibus vel caulinis et alternis; caulibus 1-10+ decumbentibus vel erectus simplicibus vel superne divaricatus; folia remota alterna simplicia vel bipinnatisecta sessilia vel longipetiolata, lamina oblanceolata vel orbicularis chartacea margine subintegra vel crenato-dentata; capitulescentia terminalis monocephala vel oligocephala cymosa; capitula radiata flosculis numerosis, involucrum campanulatum vel hemisphaericum, phyllaria herbacea paullum inaequalia pauciseriata, clinanthium epaleaceum convexum glabrum; flosculi radiati pistillati 1-4-seriati, corolla brevis rosea; flosculi disci hermaphroditi, corolla campanulata glabra quinquelobata, anthera palida apiculata; cypselae complanatae epapposae subrostratae obovatae, margines incrassatis, collum vicidum.

Small perennial herbs (rarely collected in first year and appearing as annuals), commonly with rhizomes, subscapose, remotely bracteate-leaved, or leafy to near capitula, never truly scapose; stems single or more commonly few-branched from base, often brownish red, leaves commonly basal and cauline, present at flowering, proximal ones spreading laterally, cauline leaves increasingly appressed distally toward capitula; roots fibrous; herbage with mostly patent simple non-colored trichomes. **Leaves** usually simple to infrequently bipinnatisect, alternate, often slightly rugulose adaxially, surfaces eglandular, glabrous or densely hirsute-pilose, margins crenate, toothed, to rarely deeply divided to near midrib; basal leaves few-several, typically present when flowering, usually long-petiolate; cauline leaves few-several, longer than internodes or often bracteate and remote, usually sessile. **Capitulescence** monocephalous to 1–few(–several)-capitulate in open cymes, main axis flexuous-ascending to sometimes stiffly erect, lateral branches not over-topping central axis, capitula pedunculate. **Capitula** radiate, small; involucre campanulate to hemispheric; phyllaries nearly subequal, 2–3-seriate, usually oblong, herbaceous, flat, green with thin brownish-red margins, midvein somewhat conspicuous, glabrous or sparsely pubescent, sometimes appearing pustular distally, margins ciliate and hyaline, apex usually subobtuse; clinanthium slightly convex, epaleate. **Ray florets** several–many, 1–4-seriate, pistillate, the outer ray florets with longer corollas than the inner series; corolla with limb mostly pinkish or pinkish-white to rarely ochroleucous (never yellow), fading to brownish red, weakly papillose-glandular (mostly on tube, trichomes biseriate, ca. 5-tiered) or glabrous, tube typically very short, usually only about as long as developed collar on cypselae, infrequently tube about twice as long as collar, limb directed outward, narrow, lanceolate or oblong, entire to weakly 2–3-denticulate, not lobed; style purplish. **Disk florets** relatively few and typically fewer in number than rays, bisexual, fertile and usually forming fruits; corolla campanulate, glabrous,

tube, throat, and lobes more or less subequal, characteristically 5-lobed (very rarely an occasional capitulum with a single 4-lobed corolla, never consistently 4-merous), pink fading to brownish red distally, often green proximally, lobes spreading to sometimes reflexed; anthers thecae often yellowish, rounded basally, appendages flat, apiculate, distinctly narrower than anther thecae, laterally thin-celled, endothecial tissue polarized; style 2-veined, one vein each continuing to about middle of branches (i.e., near end of stigmatic surfaces), base simple, never nodular, glabrous, immersed within small annular nectary, branches triangular-lanceolate, pinkish-red, stigmatic lines proximal, marginal but not very distinct, about as long as sterile appendage, appendage acute at apex, papillose abaxially, papillae sometimes present abaxially also on fertile portion, papillae oblong, often moderately spreading. **Cypselae** epappose, obovate (or sometimes disk cypselae subcylindrical), compressed (radially), exalate, both faces brown, rarely with midnerve visible or developed, raphide crystals not seen in pericarp, with pale-colored thickened lateral margins, rays and usually disks with narrowed apical collared (short-rostrate), collar densely glandular and sticky, collar of disk florets often smaller or in two species consistently vestigial, margins glabrous or infrequently pubescent with duplex trichomes and/or biseriate papillose glands, plants sometimes collected immature with non-fully developed cypselae in disk florets narrower than the more mature peripheral rays, infrequently disk florets not pollinated and then the sterile subcylindrical ovary nearly as long as ray cypselae.

   Typology. *Lagenophora westonii* is designated as the generitype — it has all critical generic features, i.e., it is moderately leafy stemmed, has glabrous 5-merous disk corollas, and has bisexual disk florets forming fruit. The type of *Lagenophora* sect. *Pseudomyriactis* is *L. panamensis*, the earliest named species. But Cabrera (1966) characterized (erroneously I believe) *L. panamensis* as having disk flowers "apparently mostly sterile," and it is thus not chosen as the generitype of *Talamancaster*. As such, *Talamancaster* and *Lagenophora* sect. *Pseudomyriactis* are heterotypic and not nomenclatural synonyms.

   Etymology. Although the genus ranges from the Venezuelan Andes (Fig. 9A) to the Sierra de los Cuchumatanes, Guatemala (Fig. 9B), the masculine generic name *Talamancaster* is coined to draw attention to the geographic epicenter (the Talamanca Mountains; Fig. 10) of the genus as well as its placement in tribe Astereae.

   The "core genera" (Nesom 2001) of the *Lagenophora* group of Grangeoids are mostly small herbs characterized by their 2+-seriate pistillate florets and flat viscid-collared cypselae with no pappus. Cabrera (1966) and Sancho et al. (2015) suggested such fruits could be bird-dispersed. The species are very similar to one another and are restricted to geologically relatively recent Alpine mountain tops (viz Graham 2006; Van der Hammen & Cleef 1986). For example, Gregory-Wodzicki (2000) gave the final northern Andean uplift at about 2.7 mya, and Rauscher (2002) noted suggestions that páramos developed soon thereafter. Five of six species treated here in *Talamancaster* are found in the páramo ecosystem, although they are also found sporadically in wet forest and grassy or marshy areas below páramos. Islebe and Kappelle (1994) stated that the Pleistocene glaciation carved the U-shaped valleys on Chirripó in the Talamancas (Fig. 10A) and in the Cuchumatanes. Other important studies of Costa Rican páramos include those of Weber (1958) and Kappelle and Horn (2005, 2016).

   The *Lagenophora* group contains a few genera with functionally staminate disk florets, and on occasion disk florets in *Talamancaster* may not (or have been said to) set fruit. For example, see Cabrera's (1966: 305) characterization of disk florets in *T. panamensis* as "apparently mostly sterile" as compared to the Sidney Fay Blake holotype sketch of the species that is reproduced here in Figure 1. The Blake sketch instead shows an obviously fertile bisexual disk floret with a developing cypsela. Also, in the minute capitula of *T. minusculus* non-fruit forming disks may be found, but neither this nor Cabrera's statement are taken by me as more taxonomically significant than the

glabrous disk corolla character that serves to unite the species of *Talamancaster*. The genera *Rumfordia* DC. (tribe Millerieae; Sanders 1977), *Zyzyura* H. Rob. & Pruski (tribe Eupatorieae; Robinson & Pruski 2013), and *Electranthera* Mesfin, Crawford, & Pruski (Tribe Coreopsideae; Pruski et al. 2015) are 'typical' Compositae characterized by their fertile bisexual disk florets, but on occasion inner disks of these latter three genera were similarly noted not always to reach anthesis or form fruits.
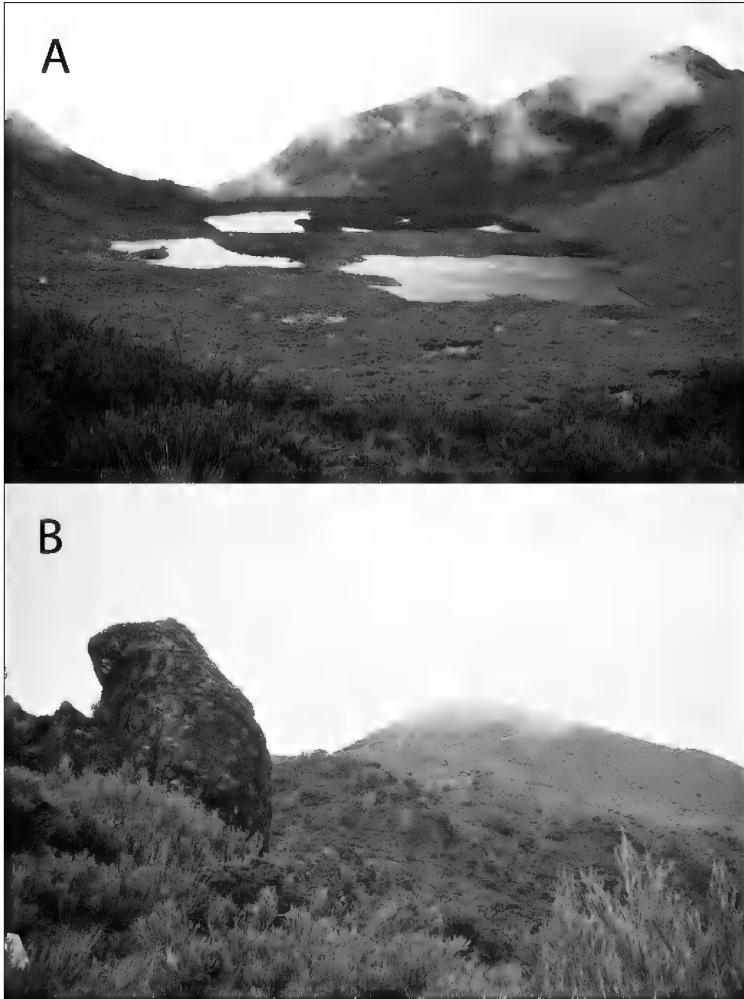

Figure 10. Grassy páramo habitats of *Talamancaster* in the Cordillera de Talamanca, Costa Rica. A. Lakes of glacier-carved U-shaped (viz Islebe & Kappelle 1994) Valle de las Morrenas, Cerro Chirripó, locality of *Pruski et al. 3945*. B. Summit (background) of Cerro de la Muerte (Cerro Buenavista), locality of *Pruski et al. 3857*. *Chusquea* spp. are dominant bamboos in each páramo.
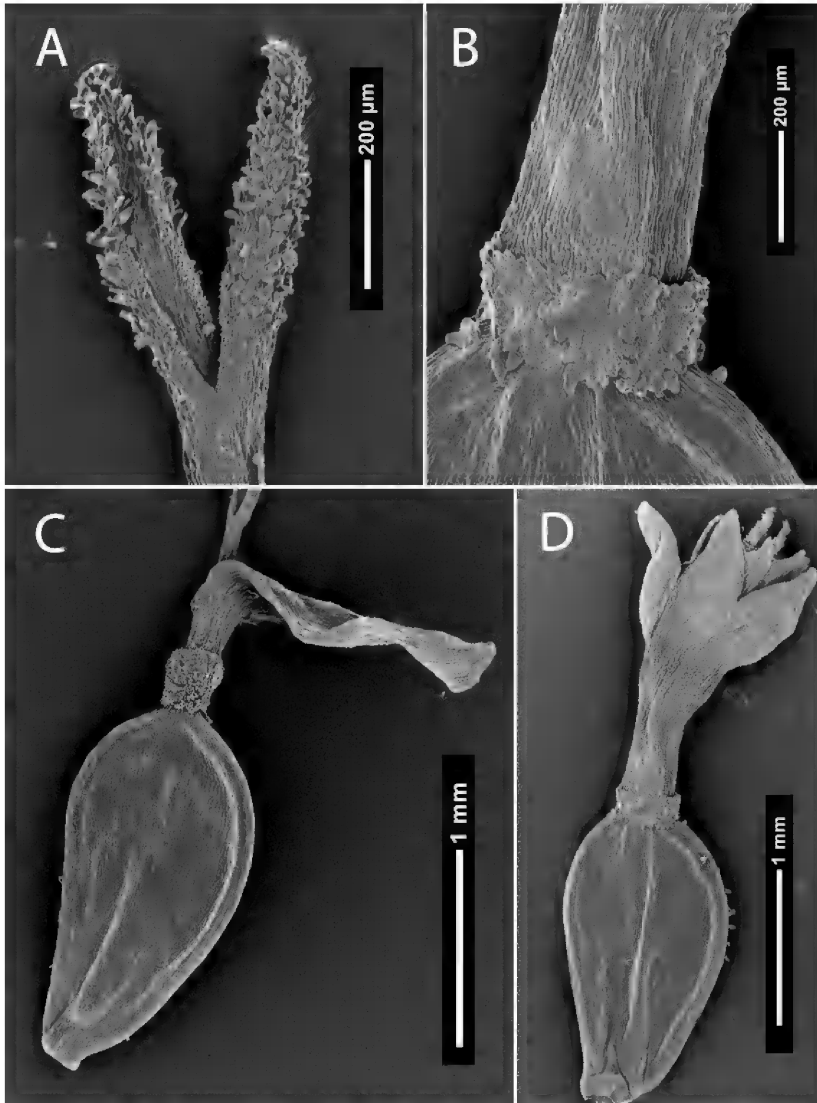
Figure 11. SEM micrographs of *Talamancaster andinus*, showing diagnostic generic characters. A. Disk floret style branches, adaxial (inner) face of one branch (on left) showing proximal ventromarginal stigmatic lines, and abaxial (outer) face of second branch (on right) showing collecting papillae concentrated on sterile apical appendage. B. Close-up of glandular collar of disk floret. C. Ray floret showing compressed cypsela with viscid-glandular collar. D. Bisexual disk floret showing the glabrous, 5-lobed, campanulate corolla and maturing fruit with collar. The abaxial marginal rib (on right) of the cypsela is pubescent with duplex trichomes and biseriate papillose-glands. (*Pruski et al. 3935*, MO).
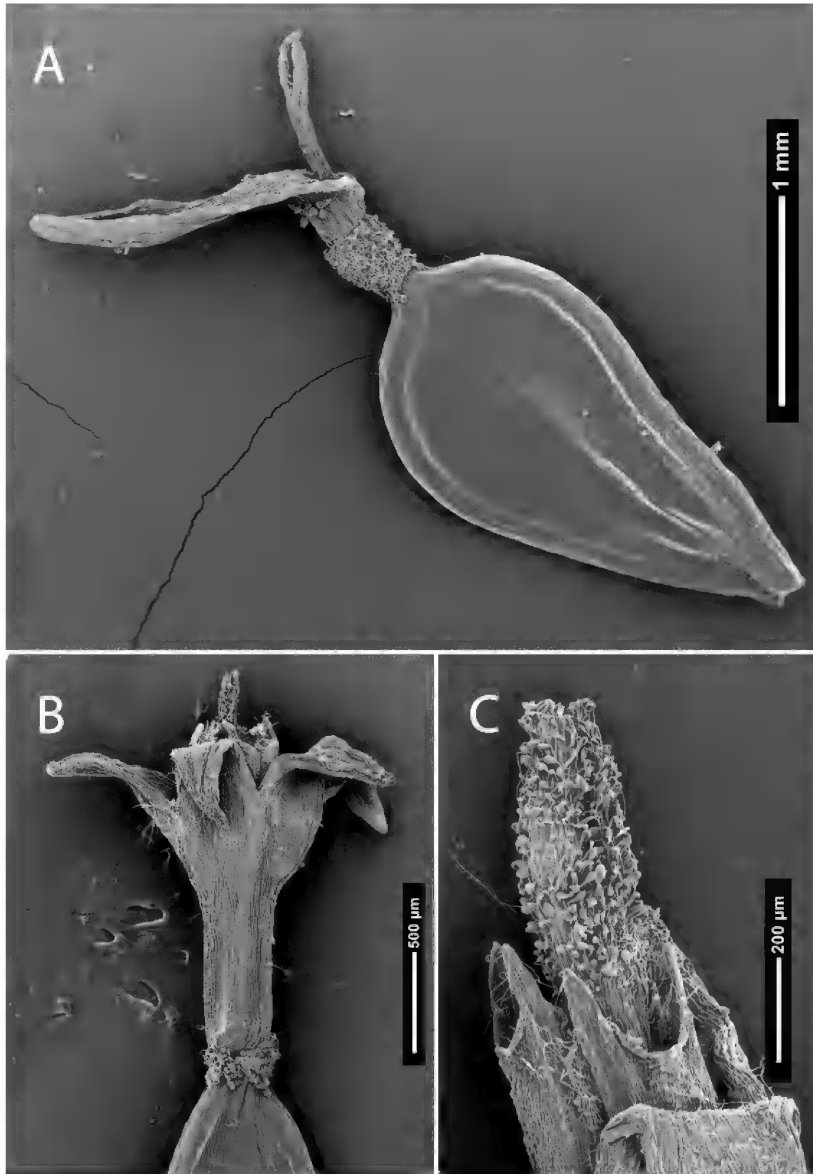
Figure 12. SEM micrographs of *Talamancaster westonii*, the generitype, showing diagnostic generic characters. A. Ray floret with maturing compressed cypsela showing viscid glandular collar. B. Disk floret showing glabrous, campanulate, 5-merous corolla and collar of immature fruit. C. Apiculate anther appendages (left center) and style showing distal abaxial papillae. (*Weston 5867*, MO, an isotype).
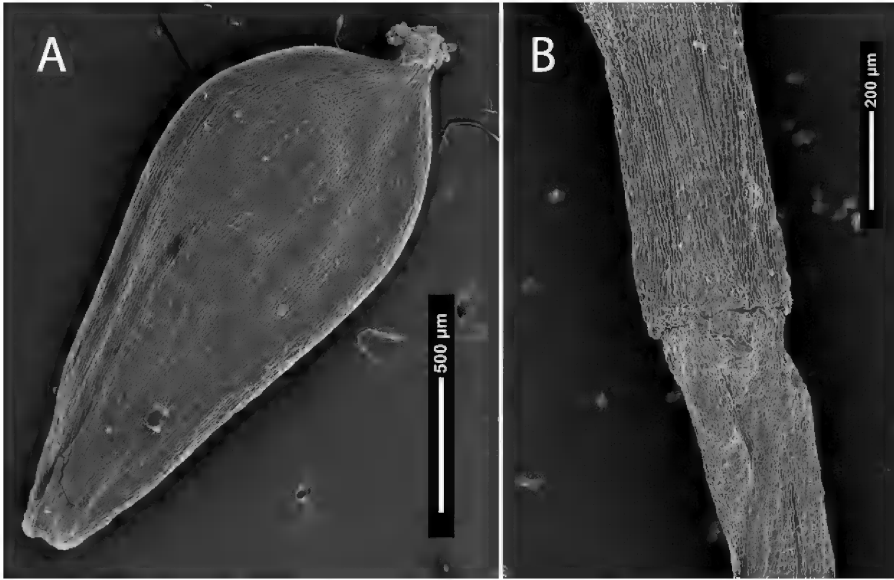
Figure 13. SEM micrographs of *Talamancaster minusculus*. A. Immature ray cypsela showing the short (much shorter than usual) glandular collar. B. Non-pollinated disk floret showing corolla tube and the cylindrical ovary without a collar; the disk ovary is about as long as ray cypsela. (*Davidse & Herrera 29400*, MO).

The leafy-stemmed vs. subscapose nature of the plants may vary but is nevertheless used as a key character below in lead 2. For example, both leafy-stemmed *Talamancaster andinus* and *T. cuchumatanicus* in late flower may have the central capitulum long-pedunculate and ebracteate, but these forms still key as leafy-stemmed because the proximal portions of the stems are leafy with leaves longer than internodes.

Among Mesoamerican Astereae, in its flat, epappose cypselae and non-yellow radiate capitula, *Talamancaster* is similar to *Astranthium* Nutt., *Bellis* L., and *Egletes* Cass. Both *Lagenophora* and *Myriactis* have been treated traditionally (e.g., Bentham & Hooker 1873; Hoffmann 1890-1894) in subtribe Bellidinae. On occasion *Talamancaster* has been identified as *Bellis*, which along with *Astranthium*, differs by cypselae neither rostrate nor apically collared. *Egletes* differs from other Central American genera by its stipitate-glandular herbage. *Lagenophora* and *Myriactis* were subsequently placed (Beaman & De Jong 1965) in Grangeinae and more recently into Lagenophorinae (Nesom 1994a; Nesom & Robinson 2007), although the phylogeny of Noyes and Rieseberg (1999) would preclude placing *Talamancaster* in Lagenophorinae.

Smith and Turner (1975) listed *Talamancaster andinus* as possibly having the Kranz syndrome. Beaman and De Jong (1965) suggested *T. cuchumatanicus* could be autogamous because of its low population density.

Talamancaster is known only from Guatemala, Costa Rica, Panama, and Venezuela (Appendix 1), but should be looked for in Mexico and Colombia. It was not reported in Colombia by Cuatrecasas (1969). A single species of *Talamancaster* is known from Guatemala and a single from Venezuela; three species are reported in Panama (one endemic); and four species are found in Costa

Rica (one endemic). Three of the six species of *Talamancaster* are single-country endemics: *T. cuchumatanicus*, *T. panamensis*, and *T. sakiranus* (Fig. 21). Two species occur in both Costa Rica and Panama: *T. minusculus* and *T. westonii*; and only *T. andinus* occurs in Costa Rica and Venezuela. Only *T. andinus* occurs in *Espeletia* páramos (Fig. 9A) and only *T. cuchumatanicus* occurs in extra-páramo alpine meadows and alpine pine forests (Fig. 9B). Five species are known from páramo and/or subpáramo vegetation (viz Figs. 9A, 10). *Talamancaster andinus* and *T. panamensis* are the only species known to occur on volcanos. The most broadly distributed species is *T. andinus*.

Many Costa Rican localities cited below are along the continental divide or on Chirripó and mostly on the borders between one of more of the following: Cartago, Limon, Puntarenas, and San Jose. The collections cited here are sometimes simply listed in alphabetic order by collector without mention of provinces.

Key to species of *Talamancaster*

1. Basal leaf blades pinnatilobed to bipinnatisect .... **6. Talamancaster westonii**
1. Basal leaf blades simple to dentate or shallowly lobed.

    2. Plants subscapose, cauline leaves proximal, remote and bracteate; disk cypselae without collars.

        3. Basal leaf blades glabrous, narrowly obovate to spatulate, base long-attenuate; southern Talamancas. .... **3. Talamancaster minusculus**
        3. Basal leaf blades hirsute-pilose, ovate, bases short-attenuate; Cerro de la Muerte and Cerro Sakira. .... **5. Talamancaster sakiranus**

    2. Plants leafy-stemmed; disk cypselae with collars.

        4. Leaf blades glabrous or sometimes blade margins or petiole margins sparsely long-ciliate; Volcán de Chiriquí, Panama .... **4. Talamancaster panamensis**
        4. Leaf blades abaxial surface hirsutulous to pilose or villous, adaxial surfaces sometimes subglabrous (*T. cuchumatanicus*) or hirsutulous to pilose or villous; Guatemala, Costa Rica, and /or Venezuela.

            5. Ray florets 2-seriate; leaf blades hirsutulous to pilose or villous adaxially; Costa Rica and Venezuela .... **1. Talamancaster andinus**
            5. Ray florets 1-seriate; leaf blades subglabrous adaxially; Guatemala .... **2. Talamancaster cuchumatanicus**

1. TALAMANCASTER ANDINUS (V.M. Badillo) Pruski, **comb. nov.** *Lagenophora andina* V.M. Badillo, Darwiniana 7: 331. 1947. *Myriactis andina* (V.M. Badillo) M.C. Vélez, Mitt. Bot. München 17: 38. 1981. **TYPE: VENEZUELA. Mérida.** Laguna Mucubají, 3600 m, 21 Jul 1944, *Steyermark 57501* (holotype: VEN; isotypes: F, MO, NY, US). Figs. 7–8, 11, 14–17.

Perennial leafy-stemmed (at least proximally) herbs 7.5–18 cm tall, not subscapose; stems ascending, 1-6 from base, leaves in basal rosettes but stems leafy with leaves only slightly smaller to near capitula, villous. **Basal leaves** long-petiolate, blade 2.5–5 × 1.3–2.5 cm, ovate to elliptic, surfaces villous, base short-attenuate, margins 7–8-toothed, apex subobtuse, petiole 3–5 cm; cauline leaves 1.5–3 × ca. 0.4-0.8 mm, sessile, surfaces hirsutulous to pilose-villous, base clasping, vaginate, margins 1–3-toothed, apex subobtuse to obtuse. **Capitulescence** in cymes, 1–4-capitulate, ultimate capitulum sometimes held above distal most cauline leaves, at least capitula on lateral branches

mostly held within stem leaves as pressed and seen on herbarium sheets; peduncles 3–30 mm long, sparsely villous. **Capitula** (40-)50–72-flowered; involucre 4–6 × 5–7 mm, hemispheric, sometimes moderately closely subtended by very small bracteate leaf partly overlapping phyllaries but more acute than phyllaries; phyllaries subequal or the outermost shorter, 2–3-seriate, 3.5–6 × 0.8–1 mm, relatively narrowly acute to nearly obtuse. **Ray florets** (25–)35–55, 2-seriate; corolla 1.5–2.2(–2.6) mm long, glabrous or sometimes weakly papillose abaxially at tube-limb juncture, tube 0.3–0.4(–0.8) mm long, white to brownish-purple, glabrous or glandular, limb ca. 1.5-1.8 mm long, apex bidentate. **Disk florets** 15-17; corolla (4–)5(–6)-lobed, 1.8-2.1 mm long, yellow-green, lobes 0.6–0.9 mm long; anthers small, 0.4-0.5 mm long. **Cypselae** 1.5–2 mm long, cypselae of rays and disks more or less similar, body glabrous or very rarely papillae 50 μm long or twin trichomes ca. 70 μm long, collar in rays 0.3-0.4 mm long, collar in disks to ca. 0.2 mm long.

Figure 14. Line drawing of *Talamancaster andinus*, showing collars on both ray and disk cypselae. (Reproduced from Aristeguieta 1964: 258, t 30 as *Lagenophora andina*).

Figure 15. Habit photograph on Cerro de la Muerte (Cerro Buenavista) of *Talamancaster andinus*, showing the leafy, erect or prostrate stems. (*Pruski et al. 3857*).

Distribution and ecology. *Talamancaster andinus* is the most widespread species of *Talamancaster*. It is the only species to occur in *Espeletia* páramos (Mérida, Venezuela) and the only Costa Rican member found on volcanos. The species flowers mostly from July–September at about 2900–4000+ meters elevation.

Representative collections examined. COSTA RICA. Cerro de la Muerte, 3400–3500 m, 25 Jul 1945, *Holm & Iltis 597* (MO); Floor of the crater of Turrialba Volcano, 3200 m, 26 Jul 1965, *Lent 674* (MO); Cordillera de Talamanca, Cerro de la Muerte (Cerro Buenavista), 3400 m, 9 Sep 2004, *Pruski et al. 3857* (INB, LP, MO); between Cerro Jaboncillo and Cerro Estaquero, 2960 m, 9 Sep 2004 (late fr), *Pruski et al. 3873* (INB, LP, MEXU, MO); Cerro Chirripó, Valle de los Conejos, 3500 m, 15 Sep 2004, *Pruski et al. 3915* (INB, MO); Cerro Chirripó, Crestones, 3460 m, 15 Sep 2004, *Pruski et al. 3926* (INB, LP, MO); Cerro Chirripó, slightly north of Cerro Pirámide, 3640–3660 m, 16 Sep 2004, *Pruski et al. 3935* (INB, LP, MO, NY, USM, VEN); Cerro Chirripó, Valle de las Morrenas, 3475 m, 16 Sep 2004, *Pruski et al. 3945* (INB, LP, MO, US); Cerro Chirripó, Crestones, 3460 m, 17 Sep 2004, *Pruski et al. 3949* (INB, MO). **VENEZUELA. Mérida.** Laguna Negra, 1952, *Aristeguieta 978* (VEN; cited by Aristeguieta 1964); Pico de Mucunuque, 4000+ m, 26 Nov 1959, *Barclay & Juajibioy 9917* (MO, US); Laguna Negra, 3500 m, 12 Sep 1971, *López-Figueiras & Huber 8766* (MERF, US); Páramo de Muchuchies, 3630 m, 17–30 Sep 1952, *Humbert 26310* (P, US); Cordillera de los Andes, 1968–1969, *Oberwinkler 13915* (M). **Trujillo.** Tuñame–Guirigay, 3200 m, Aug 1958, *Aristeguieta 3522* (US, VEN; cited by Smith & Turner 1975).

Figure 16. Representative specimen of *Talamancaster andinus* showing fibrous roots, spreading proximal leaves, ascending distal leaves, and a few-branched flowering stem. (*Pruski et al. 3935*, unmounted duplicate).
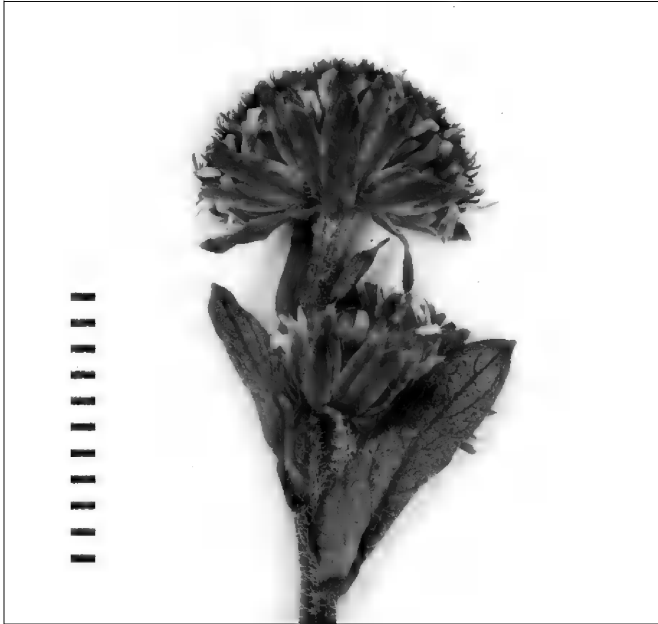
Figure 17. Capitula of *Talamancaster andinus*, the terminal capitulum showing biseriate pinkish ray corollas and nearly subequal, moderately herbaceous phyllaries, lateral capitulum on right is immature. (*Pruski et al. 3935*, unmounted duplicate). [A metric scale is towards the left].

Here I follow determinations of Jose Cuatrecasas (in sched.), who referred Costa Rican material to this singular Andean species, typified by Venezuelan material. In Costa Rica plants where the terminal capitulum is sometimes exserted, *T. andinus* often resembles *T. sakiranus* but *T. andinus* may generally be distinguished by the more densely pubescent stem leaves, disk cypselae with collar, and on average the slightly shorter ray corollas. In Venezuela, *López-Figueiras & Huber 8766* is an exceptionally robust specimen, whereas *Barclay & Juajibioy 9917* has larger than average capitula, but these are fewer-flowered than usual. The variation is not seen as taxonomically significant.

The protologue illustration of *Talamancaster andina* in Badillo (1947) shows a very narrow disk cypsela collar, but the more typical well-developed disk collar of the species is illustrated in Figure 14 (reproduced from Flora of Venezuela, Aristeguieta 1964) and Cabrera (1966: Fig. 10H). The fruits of *Oberwinkler 13915* (M) were illustrated by Vélez (1981).

2. **TALAMANCASTER CUCHUMATANICUS (**Beaman & De Jong) Pruski, **comb. nov.** *Lagenophora cuchumatanica* Beaman & De Jong, Rhodora 67: 36, pl. 1309. 1965. *Myriactis cuchumatanica* (Beaman & De Jong) Cuatr., Anales J. Bot. Madrid 42: 422. 1986. **TYPE: GUATEMALA. Huehuetenango.** Sierra de los Cuchumatanes, between Tojiah [Tojuia] and Chemal at Km 320 on Ruta Nacional 9 N, ca. 3365 m, 29 Jul 1960, *Beaman 3756* (holotype: MSC; isotypes: DUKE, F, GH, K, LP, TEX, UC, US-2). Figs. 18–19.

Low perennial leafy-stemmed herbs 8–21 cm tall from small rhizome-caudex to ca. 0.5 cm diam., usually with 3–7 basal leaves and 1–4 flowering stems from very base; roots several, to 10+

cm long, fibrous; stems decumbent or sometimes ascending, simple, pilose, trichomes mostly 0.5–0.8 mm long, often leafy to near apex with 7–12 gradually reduced cauline leaves slightly longer than internodes, less commonly leafless peduncles elongating in fruit to ca. 7 cm long. **Basal leaves** few, long-petiolate, blade 1–1.7 × 0.8–1.3 cm, elliptic-ovate to orbicular, subglabrous adaxially, abaxial surface pilose or sometimes only midrib pilose, trichomes to ca. 0.5 mm long, base rounded to narrowly cuneate, margins 3–5 crenate-dentate, apex obtuse, petiole 0.7–2.5(–3) cm long, villous, sheathing basally; cauline leaves narrowly winged-petiolar base or sessile, blade 0.9–1.8 × 0.4–0.8 cm, spatulate or obovate to oblanceolate, subglabrous adaxially, abaxial surface pilose or sometimes only midrib pilose, base subclasping or clasping, margins 1–3-toothed or distal most subentire, apex usually obtuse. **Capitulescence** monocephalous, stem leafy to near apex or sometimes greatly elongating in fruit; peduncle 0.5–3.5(–7) cm long, villous. **Capitula** 18–34-flowered; involucre 4–5 × 5–7 mm, broadly campanulate; phyllaries nearly subequal, ca. 3-seriate, subimbricate and weakly overlapping distally especially once pressed, 3.5–5 × 0.8–0.9 mm, linear-lanceolate, greenish to near thinly scarious margins, sometimes purplish apically, midrib distinct, the few secondary veins basically obscure, glabrous or outer ones sparsely pilose proximally, distal margins often weakly fimbrillate-ciliolate, apex acute to narrowly obtuse. **Ray florets** 10–20, 1-seriate; corolla 2.1–2.4 mm long, tube 0.1–0.2 mm long, obviously glandular-pubescent, limb 2–2.2 × 0.5–0.7 mm, ochroleucous or becoming purplish and reflexed with age, glabrous, apex 2–3-denticulate. **Disk florets** 8–14, bisexual; corolla 1.8–2.4 mm long, yellow-green, lobes 0.7–0.8 mm long; style branches ca. 0.6 mm long, stigmatic surface and sterile appendage subequal. **Cypselae** 2.8–3.7 mm long, rays and disks similar but ray rostrum ca. 0.4 mm long and disk rostrum ca. 0.2 mm long.

Figure 18. Low, annular nectary and immersed style base of *Talamancaster cuchumatanicus* showing two vascular bundles. (*De Jong 694*, NY). [Scale bar 0.1 mm].

Figure 19. Isotype of *Lagenophora cuchumatanica* [≡ *Talamancaster cuchumatanicus*] showing stems leafy to capitula. (*Beaman 3756*, GH).

Distribution and ecology. *Talamancaster cuchumatanicus* is endemic to alpine meadows and alpine pine forests in the Sierra de los Cuchumatanes and on the Tecúm Uman Ridge in southwestern Guatemala, where it has been collected from 3200–3365 meters elevation, flowering in July and August. The species was not found flowering by Rosa Ortiz and the author in March 2007 (off-season) when we searched for it at the type locality.

Additional collections. GUATEMALA. Huehuetenango. Sierra de los Cuchumatanes, between Chemal and Tojiah at km 319.5 on Ruta Nacional 9 N, 3365 m, 30 Jul 1960, *De Jong 694* (LP, MSC, NY, TEX); Sierra de los Cuchumatanes, 26 Aug 1961, *De Jong 1145* (MSC); Sierra de los Cuchumatanes, km 322–323, 3200 m, 27 Aug 1961, *De Jong 1147* (MSC). **Totonicapán.** On the Tecúm Uman Ridge at km 154 on Ruta Nacional No. 1, ca. 20 km E of Totonicapán, ca. 3340 m, 14 Aug 1960, *Beaman 4170* (MSC).

Talamancaster cuchumatanicus is the northernmost species of *Talamancaster* and is the sole species of the genus found well northwest of páramo ecosystems. Graham (2006) noted that uplift in the Cuchumatanes was in the Pliocene and subsequent development there of alpine habitats, however, roughly coincided with northern Andean uplift and associated development of páramo ecosystem that developed in the last 2.5 my. The species occurs in the Sierra de los Cuchumatanes and on the Tecúm Uman Ridge, which are each older geologically "than neighboring Quaternary volcanic cones" (Beaman & De Jong 1965). The species has not been found on nearby volcanos. *Talamancaster cuchumatanicus* is occasional at the type locality, but Beaman and De Jong (1965) noted that only a single plant was found on Tecúm Uman Ridge east of Totonicapán, some 100 kms SSE of the type locality.

Although most Compositae are outcrossers, Beaman and De Jong (1965) suggested, on the basis of being few-flowered with low population densities, that *T. cuchumatanicus* might be autogamous. The ray florets in species of *Talamancaster* are characteristically 2+-seriate, but in *T. cuchumatanicus* the ray florets are uniseriate. The uniseriate rays in *T. cuchumatanicus* appear to be basically a by-product of the capitula being few-flowered, and this condition is not interpreted here as generically significant. Elsewhere in *Talamancaster*, small-capitulate *T. minusculus* and *T. sakiranus* may also have uniseriate rays. Photographs of the cypselae of *T. cuchumatanicus* are found in the protologue, and fine line drawings appear in Cabrera (1966) and Nash (1976).

3. TALAMANCASTER MINUSCULUS (Cuatr.) Pruski, comb. nov. *Lagenophora minuscula* Cuatr. (as "*Lagenifera*"), Phytologia 52: 172. 1982. *Myriactis minuscula* (Cuatr.) Cuatr., Anales J. Bot. Madrid 42: 422. 1986. **TYPE: PANAMA. Bocas del Toro (as Chiriquí on label and in protologue).** Cerro Fábrega and vicinity (between Cerro Bine and north end of Cerro Fábrega ridge), near the Costa Rican frontier, 3150–3335 m, 7–8 Apr 1976, *Weston 10154* (holotype: MO). Figs. 13, 20–21.

Perennial rhizomatous subscapose herbs 3–30 cm tall; the small caudex long-fibrous rooted; roots several, to 11 cm long, in small plants sometimes longer than the aerial portion of plant; stems spreading thence quickly ascending, 1–3 from base, sparsely hirsutulous to moderately pilose distally, glabrate proximally, cauline leaves remote and bracteate. **Basal leaves** long-petiolate, blade 1–2 × 0.3–1 cm, narrowly obovate to spatulate, surfaces glabrous, base long-attenuate, margins 2–4-crenate-dentate, teeth forward-directed, apex obtuse, petiole 1–8 cm long, long-ciliate to sometimes glabrate, flattened proximally, vaginate at the base; cauline leaves 1–8, in the proximal half of stem, quickly reduced with the distal ones becoming remote, bracteate, sessile, 0.6–0.9 × 0.1–0.2 cm, oblong, often much shorter than internodes, surfaces subglabrous, base clasping, margins 1–3-toothed distally, apex broadly acute to nearly rounded. **Capitulescence** monocephalous. **Capitula** 27–41-flowered; involucre 3–4 × 4–6 mm, broadly campanulate; phyllaries subequal or the outermost shorter, ca. 3-seriate, 2.5–3.5 × 0.8–0.9 mm, glabrous, sometimes purplish distally, apex broadly acute. **Ray florets** 17–23, 1–2-seriate; corolla 2.8–3.5 mm long, white or pinkish-tinged to reddish-purple with age, glabrous or infrequently tube sparsely glandular, tube 0.4–0.5 mm long, limb 2.4–3 x 0.5–0.6 mm, submarginally 2-nerved, apex 2(–3)-denticulate. **Disk florets** 10–18, sometimes abortive; corolla 2–2.4 mm long, (4–)5-lobed, white to greenish-yellow, tube ca. 0.7 mm long, lobes 0.5–0.7 mm long; style branches 0.7–0.8 mm long, stigmatic surface usually slightly shorter than the

narrowly pointed sterile appendage. **Cypselae** 1.8–2 mm long, collar of ray florets to ca. 0.1 mm long, irregularly sparse-glandular viscid towards corolla base, cypselae of disks florets without collar.

   Distribution and ecology. *Talamancaster minusculus* is endemic to marshy páramos and scrub páramos in the Cordillera de Talamanca on Cerro Kasir in southeastern Costa Rica and near or on Cerro Itamut and Cerro Fábrega in western Panama (near the Costa Rican border). *Talamancaster minusculus* has been collected from 2950–3335 meters elevation, flowering in March–April and September.
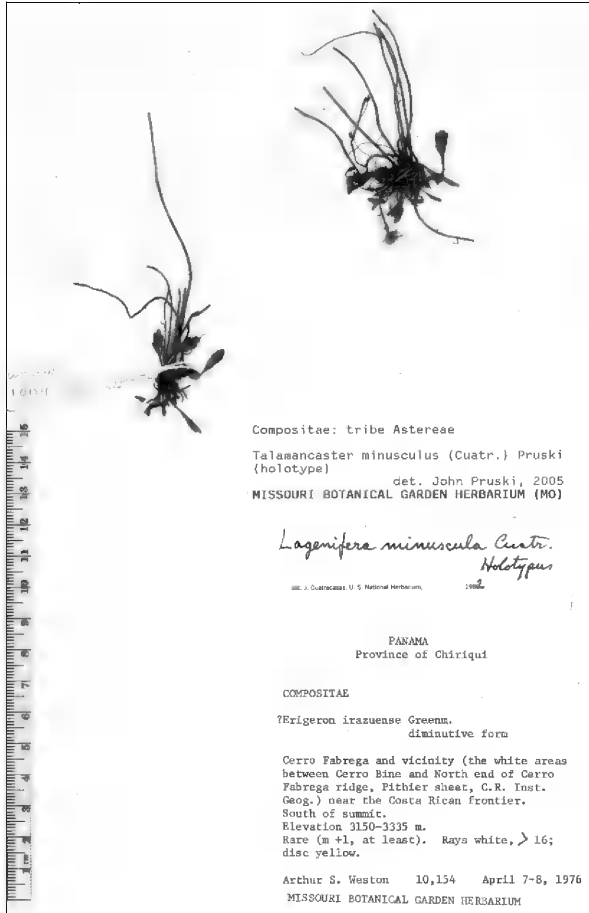
Figure 20. Holotype of *Lagenophora minuscula* [≡ *Talamancaster minusculus*] showing the diminutive habit and short, leafless scapes. The plants are mounted upside-down with the several fibrous roots extending upwards towards the top of image. These diminutive plants have equally diminutive capitula and lessened physical space for florets; the ray florets are only 1-2-seriate, and the disk florets are sometimes abortive. (*Weston 10154,* MO).
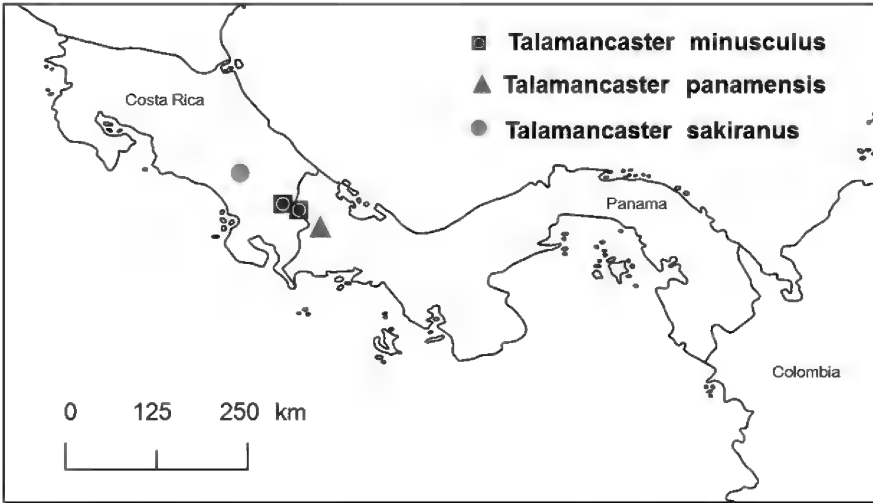
Figure 21. Distributions of regional endemics *Talamancaster minusculus*, *Talamancaster panamensis*, and *Talamancaster sakiranus* in southeastern Costa Rica and western Panama, the distributional epicenter of the genus. *Talamancaster westonii* occurs throughout much of the range of species plotted here.

Additional collections examined. COSTA RICA. Limon-Puntarenas border. Cordillera de Talamanca, Cerro Kasir, 2950 m, 22 Mar 1984, *Davidse et al. 25873* (MO); Cordillera de Talamanca, Cerro Kasir, 2950 m, 20 Sep 1984, *Davidse & Herrera 29400* (MO, US). **PANAMA. Bocas del Toro.** Between Itamut and Bine peaks, Fábrega massif, 3200 m, 5–9 Mar 1984, *Gómez et al. 22446* (CR, MO); 1–2 km SWW of Cerro Itamut camp, [Cerro Fábrega], 3175 m, 6–7 Mar 1984, *Gómez et al. 22593* (CR, MO), *Gómez et al. 22605* (CR, MO); Parque Nacional La Amistad, Cerro Fábrega, 3250 m, 18 Mar 2003, *Klitgaard et al. 843* (BM, MO, PMA).

Talamancaster minusculus has disk cypselae without apical collars but nevertheless is included in *Talamancaster* by its bisexual disk florets with glabrous, campanulate, 5-merous corollas. *Talamancaster minusculus* is distinct from similarly collarless *T. sakiranus*, although it is on average only smaller in stature, glabrous-leaved, and further to the southwest in distribution.

4. TALAMANCASTER PANAMENSIS (S.F. Blake) Pruski, **comb. nov.** *Lagenophora panamensis* S.F. Blake, Ann. Missouri Bot. Gard. 26: 314. 1939. *Myriactis panamensis* (S.F. Blake) Cuatr., Anales J. Bot. Madrid 42: 422. 1986. **TYPE: PANAMA. Chiriquí.** Volcán de Chiriquí, 2500–3380 m [presumably 2900+ m], 4–6 Jul 1938, *Woodson, Allen & Seibert 1047* (holotype: US; isotypes: GH, MO, NY, US ex NA). Figs. 1, 22–23.

Perennial rhizomatous leafy-stemmed herbs 7–26 cm tall, not subscapose; stems 1–5 from base, ascending, subglabrous to distal portions strigillose or hirsute, cauline leaves gradually reduced and overlapping in pressed specimens, slightly longer than the internodes. **Basal leaves** narrowly winged-petiolate to base, 2.5–5.5 × 0.7–1.4 cm, oblanceolate or narrowly obovate, surfaces glabrous or sometimes blade margin or petiole margin sparsely long-ciliate, base vaginate, long-attenuate with the narrow winged portion often longer than moderately expanded blade, margins 5–8-dentate, sometimes ciliate, teeth 1–2 mm deep, forward-directed, rarely petiole with a single lobe-tooth ca. 3.5 mm long, apex broadly acute to obtuse; cauline leaves often overlapping and longer than internodes,

1.5–2.5 × 0.4–0.6 cm, oblanceolate to oblong, surfaces glabrous, base clasping, margins 1–4-toothed, apex obtuse. **Capitulescence** cymose, leafy with capitula characteristically not held above leaves; peduncles 4–15 mm long, usually strigillose or hirsute. **Capitula** 1–5, ca. 85-flowered; involucre 4–4.2 × 6–8.5 mm, hemispheric; phyllaries subequal or the outermost shorter, 3–4.2 × ca. 0.8 mm, ca. 3-seriate, glabrous or subglabrous, sometimes purplish distally. **Ray florets** ca. 57, 2-seriate; corolla 2.2–2.7 mm long, glabrous tube 0.2–0.3 mm long, limb 2–2.4 mm long, glabrous. **Disk florets** ca. 28; corolla 1.6–2.2 mm long, lobes 0.6–0.8 mm long. **Cypselae** 1.8–2 mm long, glabrous, ray and disk cypselae more or less similar but the disks sometimes narrower and disk collar 0.1 mm tall, the ray cypselae with collar ca. 0.3 mm long.
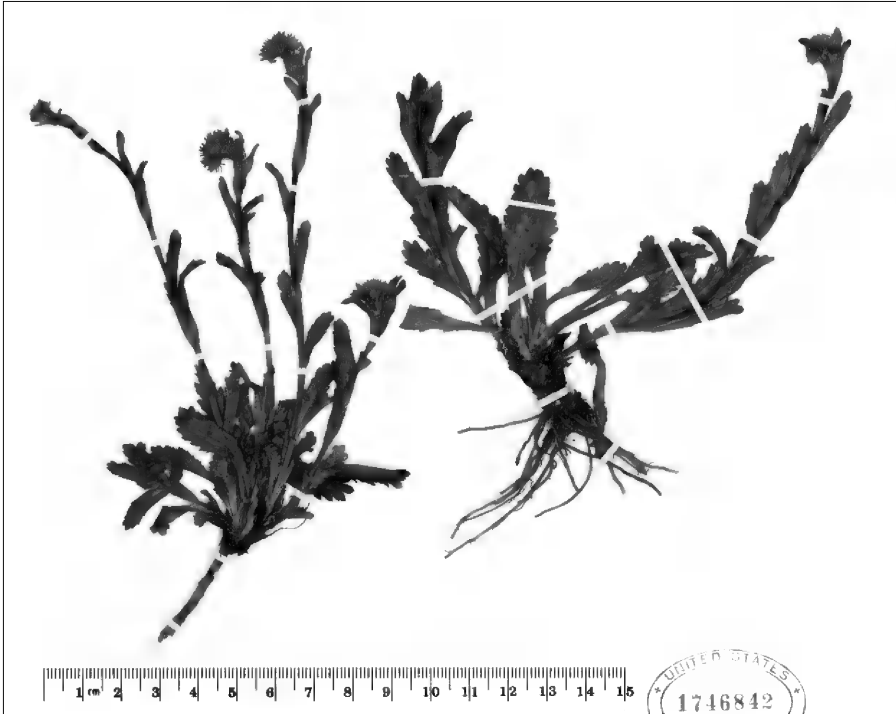
Figure 22. Holotype of *Lagenophora panamensis* [≡ *Talamancaster panamensis*] showing the stems leafy to near apex; a photograph of this specimen unmounted appears in the protologue. (*Woodson et al. 1047,* US).

Distribution and ecology. *Talamancaster panamensis* is the sole species endemic to Volcán Chiriquí (Volcán Barú) and is distinguished by its simple leaves from *T. westonii*, the other congener found (in part) on Chiriquí. The species flowers mostly in July and August seemingly from about 2900–3200 meters elevation.

Additional collections examined. PANAMA. Chiriquí. Volcán de Chiriquí, Potrero Muleto, 10400 ft. [= 3170 m], 18 Jul 1938, *Davidson 1037* p.p. (GH); Volcán Barú, bottom of 2nd crater, 3000 m, 16 Aug 1983, *Schmalzel et al. 1731 p.p.* (MO; voucher cited by Noyes & Rieseberg 1999). Both collections are mixed with *Erigeron maxonii* S.F. Blake (viz Nesom & Pruski 2011).
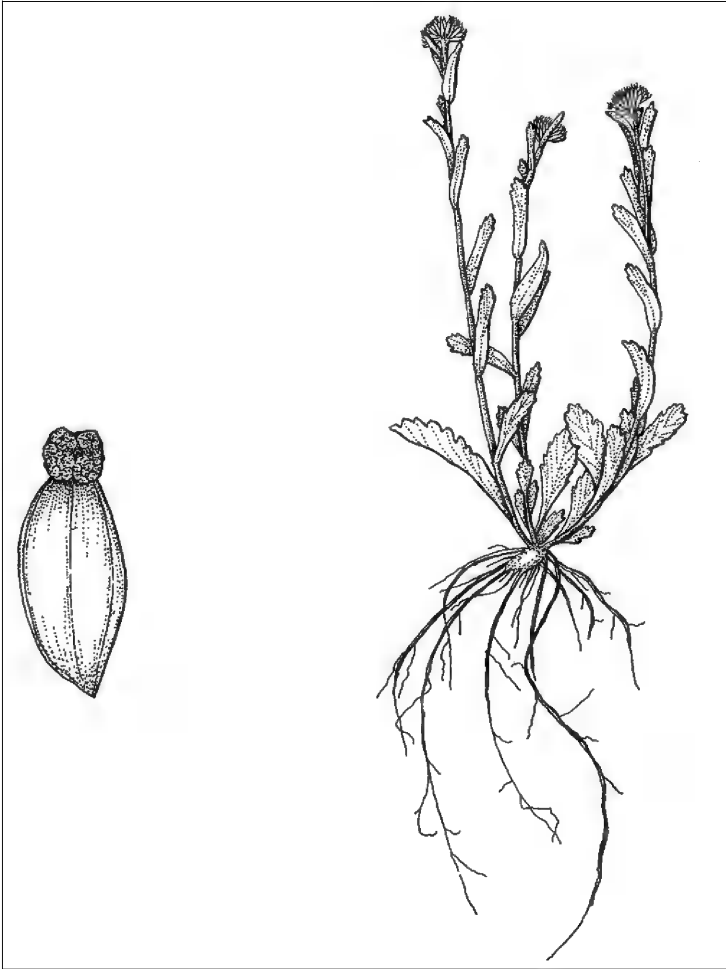
Figure 23. Line drawing of *Talamancaster panamensis* from the Flora of Panama, showing a ray cypsela with viscid-glandular collar. (Reproduced from D'Arcy 1975: 1030, t. 39 as *Lagenophora panamensis*).

    Talamancaster panamensis has simple basal leaves, and although an occasional lanceolate petiole lobe has been seen it is never consistently and obvious deep-lobed as in *T. westonii*. The two species are recognized as distinct, but they are obviously similar to each other. The report by Weston (1981) of *T. panamensis* is taken here as erroneous, and presumably is in reference to material of either *T. andinus* or *T. westonii*, the two species that are known to occur on Chirripó. I have seen Weston material from Chirripó of only *T. westonii*, although it seems equally likely that the Weston report may be based on the much more common *T. andinus*. An illustration of *T. panamensis* from the Flora of Panama (D'Arcy 1975) is reproduced here as Figure 23, and another was given by Cabrera (1966).

5. TALAMANCASTER SAKIRANUS (Cuatr.) Pruski, **comb. nov.** *Lagenophora sakirana* Cuatr. (as "*Lagenifera*"), Phytologia 52: 170. 1982. *Myriactis sakirana* (Cuatr.) Cuatr., Anales J. Bot. Madrid 42: 422. 1986. **TYPE: COSTA RICA**. Cerro Sakira, 3300 m, 14 Aug 1969, *Weston 5834* (holotype: US). Figs. 21, 24.
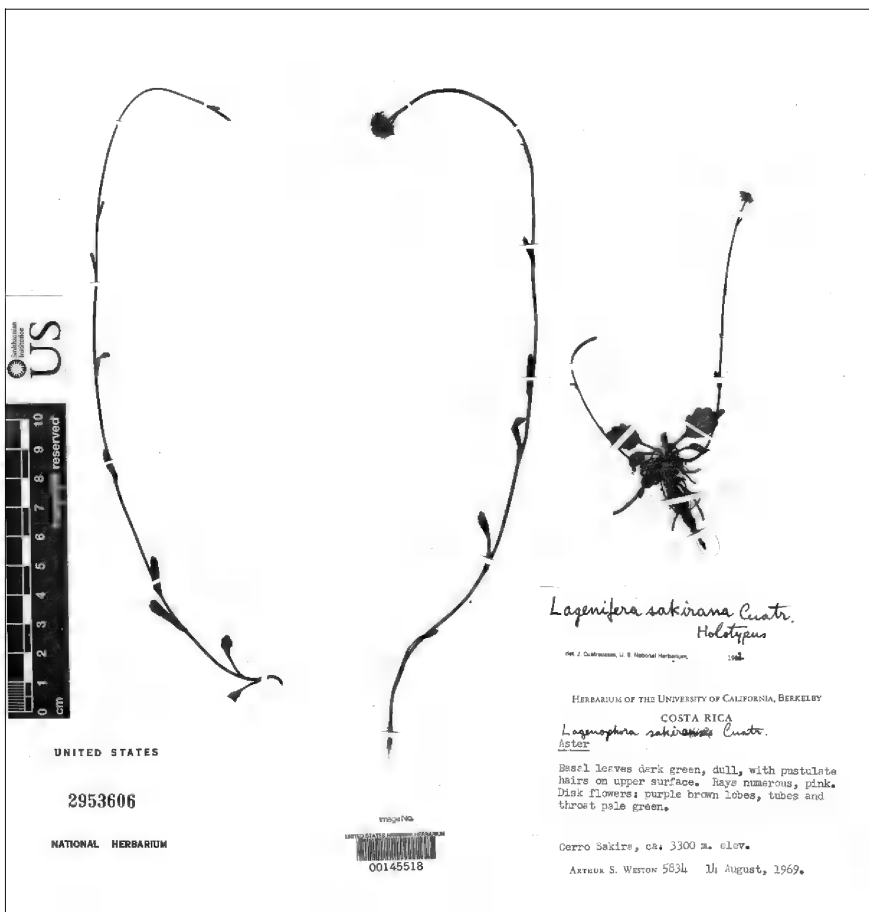
Figure 24. Holotype of *Lagenophora sakirana* [≡ *Talamancaster sakiranus*] showing the weakly leafy stems. (*Weston. 5834*, US).

Perennial rhizomatous subscapose herbs 8–25(–40) cm tall; stems ascending, 1–2 from base, sparsely pilose, cauline leaves remote and bracteate. **Basal leaves** present or absent at flowering, long-petiolate, blade 1.5–2.5 × 1–1.4 cm, ovate, surfaces hirsute-pilose, base short-attenuate, margins shortly 4–7-crenate, apex obtuse, petiole 1–3.5 cm long, pilose, vaginate basally, purplish; cauline leaves bracteate, 2-6, sessile, 0.5–2 × 0.1–0.3 cm, oblong, surfaces subglabrous, margins very sparsely ciliate, base subclasping, margins 1–2-toothed distally, apex obtuse to acute. **Capitulescence** monocephalous to much less commonly cymose with 1–2 lateral capitula, on leafless

peduncles held well above rosette leaves. **Capitula** 40–48-flowered; involucre 3.5–4.2 × 4–5 mm, broadly campanulate; phyllaries 2–3-seriate, glabrous, 3–4.2 × 0.7–1.1 mm, apex sometimes fimbriate. **Ray florets** 25–30, 1-seriate; corolla 2.1–3.1 mm long, tube ca. 0.3 mm long, glabrous or with a few glandular trichomes, limb 1.8–2.8 mm long, glabrous. **Disk florets** 15–18; corolla 2–3 mm long. **Cypselae** 2–2.2 mm long, glabrous, ray cypselae with collar 0.2–0.3 mm long, cypselae of central florets reduced, narrow, collar absent (sometimes very thinly annular), eglandular.

  Distribution and ecology. *Talamancaster sakiranus* is a rare endemic in the Cordillera de Talamanca, where it has been found on Cerro de la Muerte and Cerro Sakira. It has been collected at about 3300–3400 meters elevation flowering in August and September.

  Additional collections examined. COSTA RICA. Cordillera de Talamanca, Cerro Sakira, 3400 m, 10 Sep 2004, *Pruski et al. 3873* (INB, unicate, only one small plant found, topotype); Cerro de la Muerte, s. elev., 27 Aug 1967, *Raven 22062* (F).

6. TALAMANCASTER WESTONII (Cuatr.) Pruski, **comb. nov.** *Lagenophora westonii* Cuatr. (as "*Lagenifera*"), Phytologia 52: 169. 1982. *Myriactis westonii* (Cuatr.) Cuatr., Anales J. Bot. Madrid 42: 422. 1986. **TYPE: COSTA RICA.** Cerro Jaboncillo, 3200 m, 14 Aug 1969, *Weston 5867* (holotype: US; isotype: MO). Figs. 12, 25–27.

  Perennial leafy-stemmed herbs 17–32 cm tall, not subscapose; stems ascending, bracteate-leafy, pilose-villous, usually few-branched in the capitulescence, cauline leaves gradually reduced. **Basal leaves** long-petiolate, blade 6–7 × 2.5–3 cm, pinnatilobed to bipinnatisect, lobes oblong and subobtuse, surfaces pilose-villous to very sparsely so, margins ciliate, petiole 3–4.5 cm long, pilose-villous, vaginate at the base; cauline leaves bracteate, sessile, blade 2.5–3 × 0.4–1 cm, base clasping, the proximal cauline leaves mostly pinnatifid, the distal cauline leaves mostly 2–3-lobed, lobes oblong. **Capitulescence** in racemes or cymose or sometimes monocephalous; peduncles 5–18 mm long, pilose-villous to densely so immediately below capitulum. **Capitula** (1–)2–5, ca. 54-flowered; involucre 3.3–5 × 5.5–8 mm, campanulate to hemispheric; phyllaries 2–3-seriate, 3-5 × 0.8–0.9 mm, glabrous, apex often purplish, acute to obtuse, often slightly fimbriate or very narrowly hyaline-margined. **Ray florets** ca. 40, 2-seriate; corolla 2.2–2.8 mm long, white to purplish, tube ca. 0.3 mm long, glandular-papillose, limb 1.9–2.5 mm long. **Disk florets** ca. 14; corolla 2.2–3 mm long, yellow-green, lobes 0.6–1 mm long. **Cypselae** 1.5–3 mm long, ray and disk cypselae similar with collar well-developed, or sometimes disk collar minute and represented only by a narrow ring of viscid glands.

  Distribution and ecology. *Talamancaster westonii* is the type of the genus, and among species endemic to Costa Rica and/or Panama it has the broadest distribution. The species was described from the northwestern Cerro Jaboncillo but occurs southeast to Volcán Chiriquí (Barú) and flowers sporadically year-round, at 3000–3500 meters elevation.

  Additional collections examined. COSTA RICA. P.N. Chirripó, Sabana Los Leones, 3300 m, 30 Jan 2002, *Alfaro 3858* (INB, MO); Sabanas del Cerro Echandi, 3000–3150 m, 13 Aug 1997, *Quesada et al. 1999* (INB, MO); Valle de los Lagos, Chirripó massif, 3500 m, 7 Sep 1969, *Weston 6064* (US). **PANAMA. Bocas del Toro.** 1-2 km SWW of Itamut camp, 3175 m, 6-7 Mar 1984, *Gómez et al. 22601* (CR, MO); 2 km SW of Itamut camp, Fábrega, 3100-3200 m, 8 Mar 1984, *Gómez et al. 22645* (CR, MO). **Chiriquí.** S of Paso Respingo, N of Volcán summit, 10000–10800 ft. [= 3048–3292 m], 4 Apr 1979, *Hammel et al. 6717* (MO); E side of Volcán Barú, ca. 3000 m, 24 Jul 1975, *Mori & Bolten 7436* (MO).
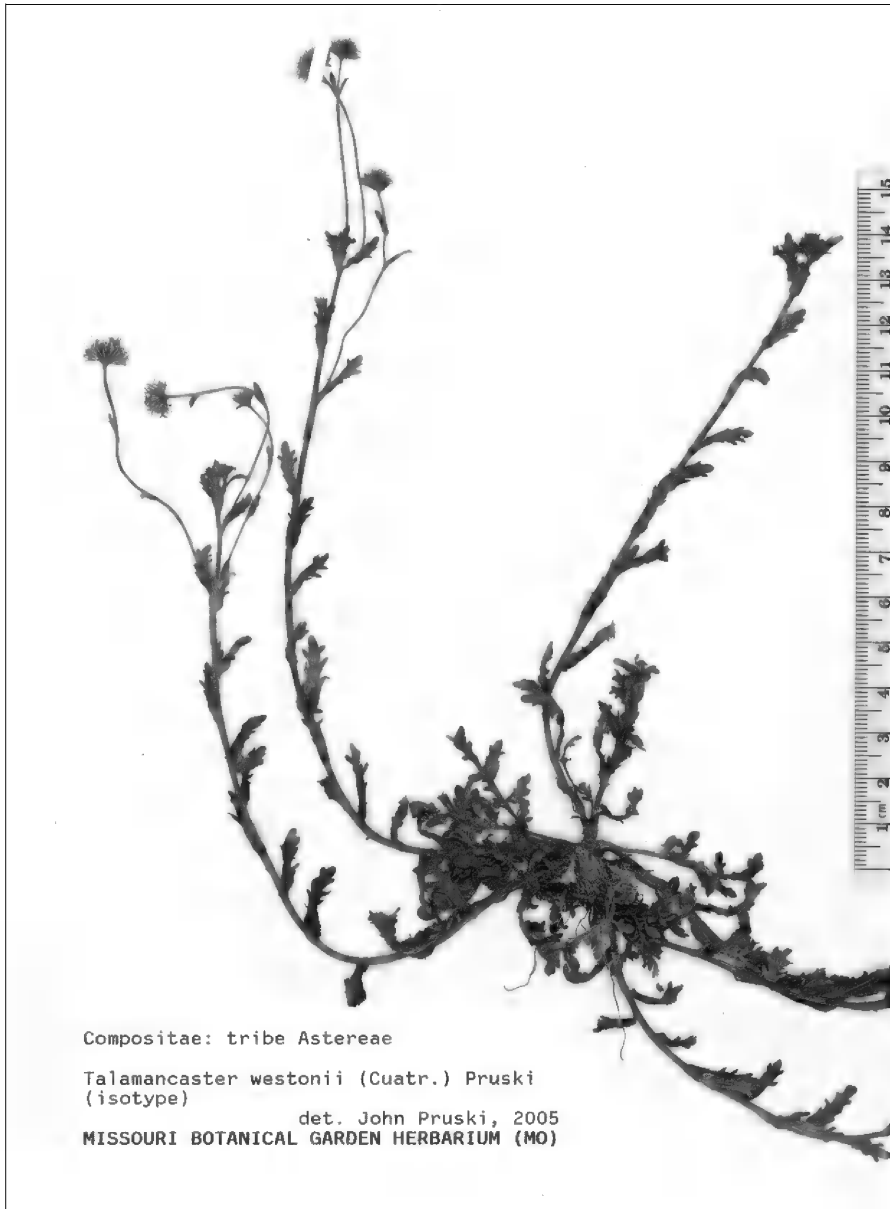
Figure 25. Isotype of *Lagenophora westonii* Cuatr., the generitype [≡ *Talamancaster westonii*]. (*Weston 5867*, MO).
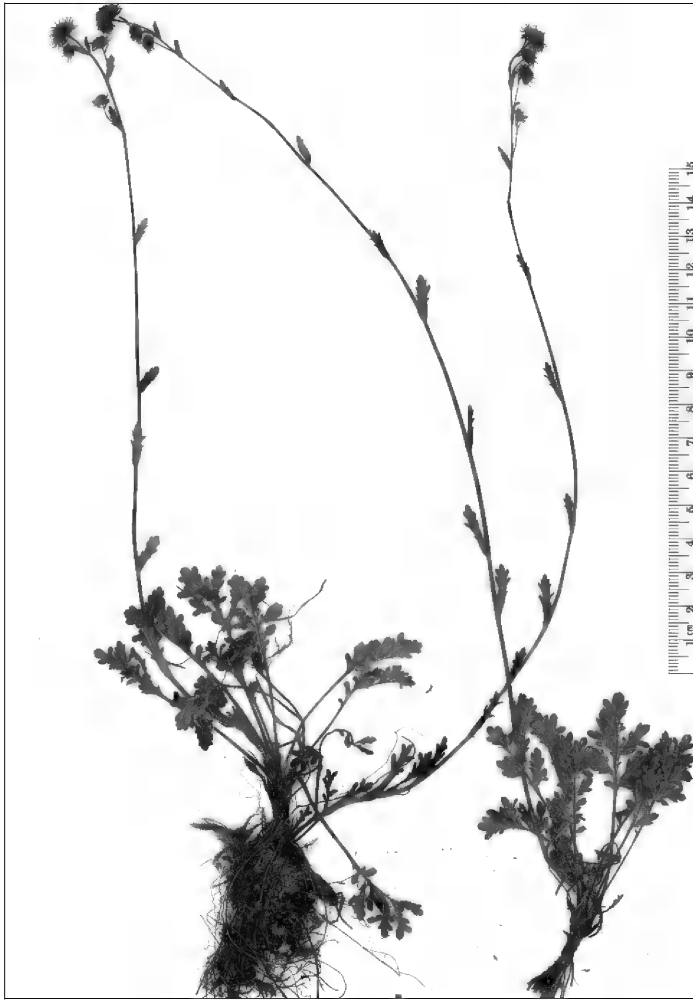
Figure 26. Representative specimen of *Talamancaster westonii* showing pinnatifid basal leaves. (*Quesada et al. 1999*, unmounted duplicate).

      Talamancaster westonii is the generitype of *Talamancaster* and is diagnosed by its pinnatisect leaves and often cymose capitulescence. The disk cypselae collar size may be variable, sometimes being hard to discern and seen only as a low ring of viscid glands. Typical *T. westonii* has deeply lobed leaves with surfaces moderately hirsute. Two collections seen from the highest reaches of Volcán Chiriquí, however, have leaves weakly pinnatilobed with subglabrous surfaces, and recall the very narrowly endemic *T. minusculus*. The low ring of disk collar glands and biseriate rays of the two odd-leaved Volcán Chiriquí collections are used to refer this material to *T. westonii*, albeit these placed there with some hesitancy.
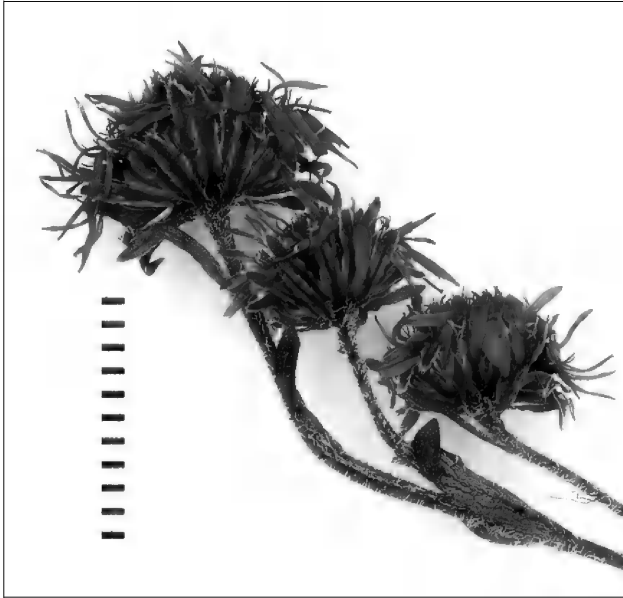
Figure 27. Capitula of *Talamancaster westonii*, showing biseriate ray florets and nearly subequal, moderately herbaceous phyllaries. (*Quesada et al. 1999*, unmounted duplicate). [A metric scale is towards the left].

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APPENDIX 1. Localities (from NW to SE) and reported *Talamancaster* species.

Guatemala: Cuchumatanes, Tecúm Uman Ridge (Pine forests)	*Talamancaster cuchumatanicus* (endemic to Guatemala)
Costa Rica: Volcán Turrialba	*Talamancaster andinus*
Costa Rica: Cerro Jaboncillo, Cerro Sakira	*Talamancaster andinus* *Talamancaster sakiranus* (endemic to Costa Rica) *Talamancaster westonii*
Costa Rica: Cerro de la Muerte (Cerro Buenavista)	*Talamancaster andinus* *Talamancaster sakiranus* (endemic to Costa Rica)
Costa Rica: Cerro Chirripó	*Talamancaster andinus* *Talamancaster westonii*
Costa Rica: Cerro Kasir	*Talamancaster minusculus*
Costa Rica: Cerro Echandi	*Talamancaster westonii*
Panama: Cerro Fábrega, Cerro Bine, and Cerro Itamut (these peaks are only a few kms from Costa Rican Cerro Echandi)	*Talamancaster minusculus* *Talamancaster westonii*
Panama: Volcán de Chiriquí (Volcán Barú)	*Talamancaster panamensis* (single locality endemic) *Talamancaster westonii*
Venezuela: Mérida, Trujillo (*Espeletia* páramos)	*Talamancaster andinus*

NEW SPECIES OF *ESCHWEILERA*
AND A FIRST RECORD OF *CARINIANA* (LECYTHIDACEAE) FROM PANAMA

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ABSTRACT
Eschweilera jefensis J.E. Bat. & S.A. Mori, **sp. nov.**, and **E. roseocalyx** J.E. Bat., S.A. Mori, & J.S. Harrison, **sp. nov.,** from the cloud forests of Central Panama are described and illustrated. Information on distribution, ecology, phenology, pollination, dispersal, and conservation status is provided. *Eschweilera jefensis* is morphologically similar to *E. sessilis*, with which it has been confused. *Eschweilera roseocalyx* is only known by a single tree from which both flowers, fruits, and seeds have been collected. Both species are known from the Cerro Jefe area but *E. jefensis* is very common there and has also been recorded at lower elevation along the El Llano-Carti Road. **Cariniana pyriformis**, formerly documented only from South America, is reported as the first species of the genus documented by a herbarium collection from Central America. A key to the Central American genera of Lecythidaceae is presented.

The Lecythidaceae are ecologically important members of Neotropical forests, where they are especially abundant in lowland, non-flooded forests of Amazonia (Mori et al. 2001; Mori et al. 2017). Central American Lecythidaceae are also common in lowlands but recent collections from higher elevations indicate that more species of *Eschweilera* occur in premontane or cloud forests than anticipated. *Eschweilera* is the most diverse and widely distributed genus of the Lecythidaceae with 77 species (not including the 7 species of the *E. tetrapetala* clade, which do not possess the morphological features of *Eschweilera* [Huang et al. 2015]). This genus ranges from Veracruz, Mexico, to southern Brazil (Mori et al. 2017).

Eschweilera was divided into the following four sections by Mori & Prance (1990) based on morphological data: (1) sect. *Bracteosa* S.A. Mori; (2) sect. *Jugastrum* Prance & S.A. Mori; (3) sect. *Tetrapetala* S.A. Mori; and (4) sect. *Eschweilera*. Studies based on molecular data (Mori et al. 2007; Huang et al. 2015) found no evidence for recognizing the first two sections and suggested that the *E. tetrapetala* clade merits recognition as a separate genus. Huang et al. (2015) hypothesized that *Eschweilera sensu stricto* consists of the *E. integrifolia* and *E. parvifolia* clades, which are both distributed in Mesoamerica and South America. The *E. parvifolia* clade is widely distributed over the New World tropics whereas the *E. integrifolia* clade has two species east of the Andes (*E. andina* (Rusby) J.F. MacBr. and *E. ovalifolia* (DC.) Nied.) and approximately 17 other species associated with Andean and Central American cloud and lowland forests throughout the range of the clade from Costa Rica to Ecuador (Mori et al. 2017). In Panama, there are approximately 17 described species of *Eschweilera*, with about one-third of them belonging to the *E. integrifolia* clade.

The two new species of *Eschweilera* described in this paper are from the Cerro Jefe region of Panama. This relatively low cloud forest area, located in the Chagres National Park, has 1016 species of flowering plants reported of which 181 (18%) have been collected only from this region (de Sedas et al. 2009). Of the 1260 endemic species of vascular plants of Panama, 222 (almost 18%) are in the Cerro Jefe area, and 66 (almost 5.2%) are unique to this cloud forest (de Sedas et al. 2009). The great endemism of the area may be due to the combination of two factors: (1) the relative isolation of the Cerro Jefe summit and (2) that it was one of the first areas to emerge before the formation of the Isthmus of Panama (Lewis 1971; de Sedas et al. 2009).

The new record of *Cariniana pyriformis* for Panama was collected from lowland rainforests in the vicinity of the Marraganti River in the Province of Darién near the border with Colombia. These forests have not been well explored so we expect that additional species of trees already documented in adjacent Colombia will eventually be discovered in Panama.

ESCHWEILERA JEFENSIS J.E. Bat. & S.A. Mori, **sp. nov. TYPE: Panamá**. Provincia de Panamá, Parque Nacional Chagres, Alrededores de Cerro Jefe, 9°12' N 79°22' W, altura 900 m, 24 Ene 1996, *C. Galdames et al. 2414* (holotype: PMA; isotypes: MO, NY, SCZ). Figures 1–3, 8.

Trees of the understory 5–15 (–20) m tall. **Bark** fissured, the outer surface gray, the outer bark laminated. **Leaves:** petioles 2–11 mm long, canaliculate adaxially, blackish when dry; blades usually elliptic, infrequently ovate, 3.2–14.5 x 1.5–7.5 cm, coriaceous, glabrous, blackish punctuations, abundant and conspicuous abaxially (even without magnification), the base acute to obtuse, the margins entire, the apex acute to acuminate; secondary veins in 8–12 pairs, plane abaxially. **Inflorescences:** from branches below leaves (ramiflorous), axillary, or terminal (suprafoliar), once branched paniculate arrangement of racemes, often scarcely branched or infrequently unbranched, the principal rachis 2.5–16.5 cm long, rough, with white lenticels; pedicel/hypanthium 2–10 mm long, slightly tapered to articulation, puberulous, slightly to markedly lenticellate, the lenticels white. **Flowers:** 2.5–4 cm diam.; hypanthium puberulous; calyx-lobes 6, ovate, 1.5–3 x 2–3 mm, horizontally oriented at anthesis, the bases not imbricate; petals 6, 15–20 x 15–12 mm, pink of various intensity, speckled with white; stamens with clavate filaments; androecial hood triple-coiled, yellow, especially near opening into flower); style narrowly obconical. **Fruits:** globose to depressed globose, 2.5–7 (including operculum) x 2.5–7.5 cm; calycine ring conspicuous, the infracalycine zone dark-brown, rounded to pedicel/hypanthium, lenticels white when fruits dry; the supracalycine zone erect, dark-brown, lenticellate, the operculum convex, sometimes umbo slightly developed, lenticellate. **Seeds** 1–7 per fruit, globose, 2.5–4.5 x 2–4.5 cm; aril spreading, white.

Ecology and Distribution. *Eschweilera jefensis* is endemic to the central and eastern parts of Panama Province, Panama (Fig. 8) where it is small trees most commonly found in cloud forest between 800 and 1000 meters. *Colpothrinax aphanopetala* R. Evans (Arecaceae) is a conspicuous co-dominant with this species (Fig. 7). In addition, specimens have been collected between 350 to 400 m from the lowland moist forests along the El Llano-Carti Road (e.g., *Dressler et al. 3543* and *S. A. Mori et al. 7728*).

Phenology. Flowers have been collected in April to August and infrequently in January (*Galdames 2414*) and fruiting has been documented from March (*Hernández 209, Galdames et al. 3769*) to July (*Batista et al. 1076, 1077*).

Pollination and dispersal. There are no observations of pollinators visiting the flowers of this species. However, other species of *Eschweilera* have been reported to be pollinated by bees

Figure 1. Holotype of *Eschweilera jefensis* archived at the University of Panama Herbarium (PMA). Photo by the University of Panama Herbarium.
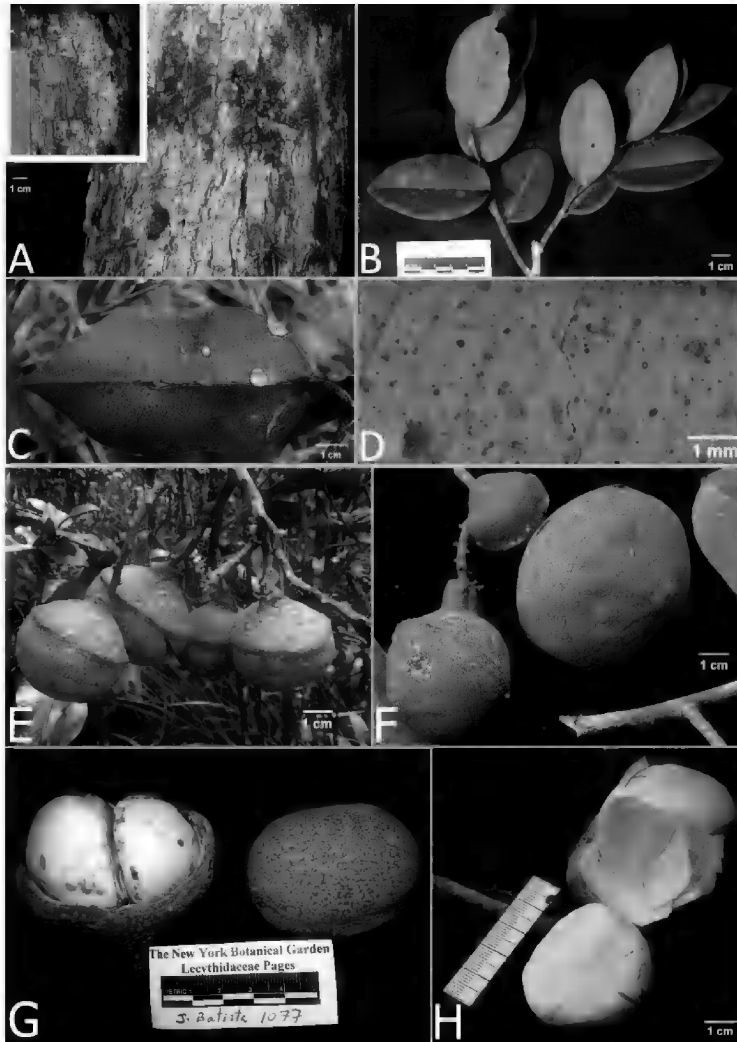
Figure 2. *Eschweilera jefensis*. **A**. Bark Irregularly fissured, grayish, the slash thick, laminated. **B.** Leaf blades usually elliptic, less commonly slightly ovate. **C.** Abaxial view of blade surface showing black punctations (visible without magnification). **D.** Close-up of black punctations on abaxial leaf blade surface. **E.** Four mature fruits with conspicuous calycine rings. **F.** Lateral view of immature and mature fruits. **G.** Open fruit showing white aril beginning to surround seeds. **H.** Seeds showing spreading aril completely surrounding seeds. Vouchered by *Batista et al. 1076* [A, B, D], 1077 [E. G], and *F. Hernández et al. 209* [C, F, H]. Photos by J. Batista [A, B, D, E, G], and R. Carranza [C, F, H].
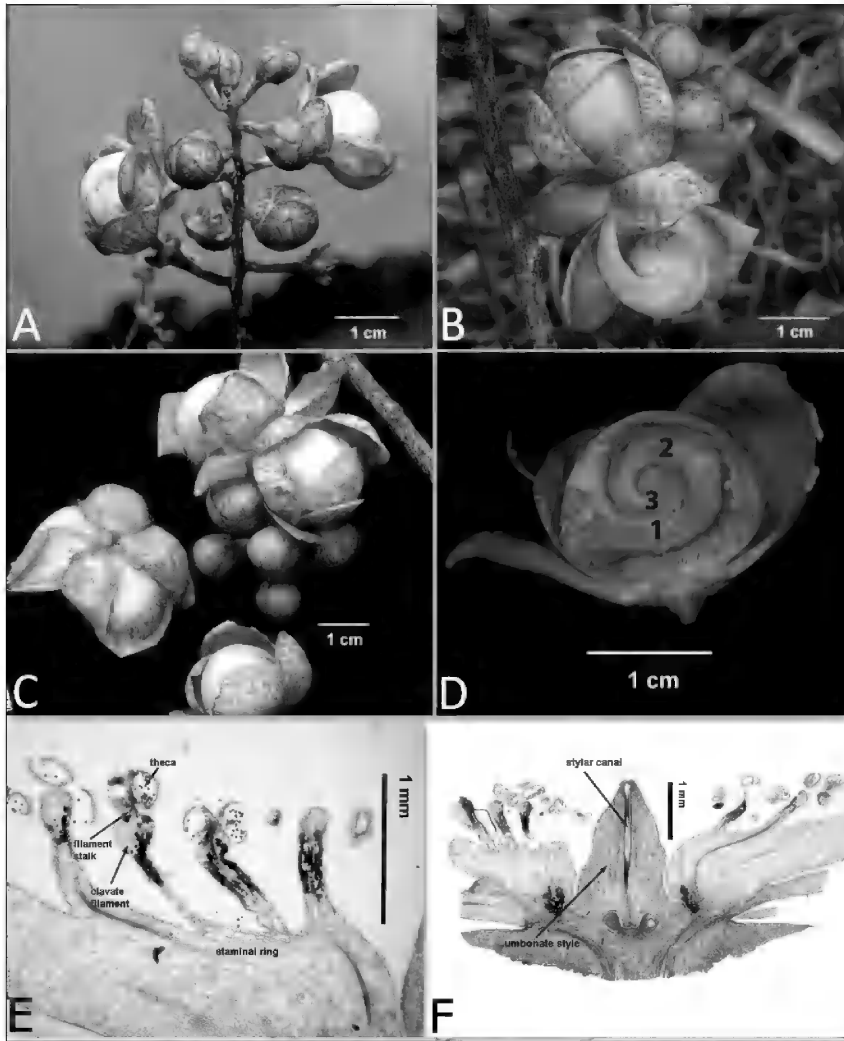
Figure 3. *Eschweilera jefensis*. **A**. Upper part of an inflorescence. The pedicel/hypanthium is elongate and slightly tapered to the articulation. **B**. Flowers are sometimes congested. **C**. Flowers and buds showing small, non-imbricate calyx-lobes in the basal view of the flower on the left. **D**. Medial longitudinal section of an androecial hood showing three coils. **E**. A stamen showing a clavate filament. The anther is attached to the filament on a constricted stalk. **F**. Pistil showing the obconical style and the stylar canal. This type of ovary is sometimes called half-inferior but we consider it as inferior because it is only the expanded style that protrudes beyond the ovary. Note that the ovules are in a single row, a feature only found in *Eschweilera*. Vouchered by *S.A. Mori et al. 8077* [A], *7728* [E, F], *F. Hernández et al. 209* [B], *C. Galdames et al 5779* [C, D]. Photos by S.A. Mori [A], R. Carranza [B], C. Galdames [C, D], and C. Carollo Matos [E, F].

(Gamboa-Gaitán 1997; Mori & Boeke 1987). Likewise, there are no observations of dispersal agents dispersing the seeds. However, it is likely that the spreading aril surrounding the seeds attracts animals that carry away the seeds.

Etymology. The epithet refers to Cerro Jefe where it is a common tree in cloud forest.

Conservation Status. *Eschweilera jefensis* is known from four localities, three in the Chagres National Park and another located along the Llano-Carti Road. Some localities in the Chagres National Park are threatened by housing developments and the Llano-Carti area, which falls outside of the national park, is converted to pasture for livestock grazing. These localities have an Extent of Occurrence (EOO) 199.2 km^2 and Area of Occupation (AOO) 36 km^2. According to the IUCN (2012) criteria, *E. jefensis* is considered Endangered [EN B1ab(i,ii,iii,iv,v) +2ab(i,ii,iii,iv,v).

Discussion. This species is characterized by its small stature; usually elliptic, medium-sized, coriaceous leaf blades with abundant black punctations abaxially; a pedicel/hypanthium tapered from the hypanthium to articulation (not truncate); medium-sized flowers; calyx-lobes ovate, small, not imbricate; petals pink, often with patches of white; androecium triple-coiled, the hood is light yellow; style thick, narrowly obconical; fruits globose to depressed globose, the operculum convex or infrequently with slightly developed umbo; and the arils spread over seeds when mature.

The Panamanian populations of *Eschweilera jefensis* have been misidentified as *E. sessilis* A.C. Sm. (Mori & Prance 1990). The type of *E. sessilis* (*A.E. Lawrance 239 NY*) was collected from cloud forest at 2100 m elevation in Andean Colombia. *Eschweilera jefensis* differs from the type of *E. sessilis* in its coriaceous leaf texture (vs. chartaceous leaf texture), very high density of dark punctuations on the abaxial leaf blade surface (vs. few punctuations), and plane tertiary veins abaxially (vs. salient tertiary veins abaxially). The new species belongs to the *E. integrifolia* clade (Huang et al. 2015) because it possesses a triple-coiled androecial hood and a spreading aril common to this clade.

Additional specimens examined. PANAMA. Provincia de Panamá, Corregimiento de la 24 de Diciembre, Cerro Jefe, La Eneida, 12 Jul 1968, *Dressler 3543* (NY, PMA); una milla después de la Eneida, región de Cerro Jefe, 9°11'19" N, 79°23'01" W, ca. 700 m, 8 de Ago 1968, *Correa & Dressler 956* (F, MO, NY, PMA, SCZ); premontane wet forest along new El Llano-Carti Road, 8–12 km N of El Llano, 400–450 m, 12 Dec 1973, *Nee et al. 8748* (MO, NY, PMA); El Llano-Carti Road, 12.5 km from inter-American hwy, ca. 350 m, 25 May 1975, *Mori & Kallunki 6358* (MO, NY, PMA); El Llano-Carti Road, 8–11 km from Inter-American hwy, tropical moist forest, 9°16' N, 79°00' W, 392 m, 13 Aug 1975, *Mori 7728* (MO, NY, PMA); cloud forest dominated by *Clusia* spp. and *Colpothrinax aphanopetala*, premontane rain forest, ca. 1000 m alt, 29 Aug 1975, *S. Mori 8007* (MO, NY, PMA); forested slopes near radio tower 9°15' N, 79°30' W, 950 m, 11 Oct 1985, *McPherson 7142* (MO, NY, PMA); vicinity of Cerro Jefe, forest slopes, 9°15' N, 79°30' W., ca. 650 m, 27 Aug 1986, *McPherson 9996* (MO, NY, PMA); near Summit, along road to east about a quarter mile below tower, 9°15' N, 79°30' W, 794 m, 8 Jul 1987, *McPherson 11170* (MO, NY, PMA); road to right about 0.5 mi below tower, 9°15' N, 79°30' W, 864 m, 13 Apr 1988, *McPherson 12446* (MO, NY, PMA); along Summit road and trail into Chagres Valley, forested slopes, 9°15' N, 79°30' W, 900 m, 10 May 1991, *McPherson & Hensold 15294* (MO, NY, PMA); Altos de Pacora, 09°14' N, 079°21' W, altura 805 m, 21 Mar 1997, *Galdames et al. 3769* (MO, PMA, SCZ); a orillas de la carretera en Altos de Pacora, cerca del caserío, 9°14'33" N, 79°21'10" W, 825 m, 29 Mar 2007, *Hernández et al. 209* (MO, NY, SCZ); en la entrada de la calle que va hacia Altos de Pacora, propiedad privada, 9°11'51" N, 79°24'16" W, 996 m, 2 May 2007, (DNA Voucher), *Hernández et al. 317* (NY, PMA, SCZ); entrando por Altos de Cerro Azul, 9°11'51" N, 79°24'16" W, altura 996 m, 2 May 2007, *Hernández et al. 331* (PMA); finca privada al lado del camino, 9°11'51" N, 79°24'16" W, 950 m, 17 Jul 2014, *Batista &*

Montenegro 1076 (NY, PMA); bosque achaparrado, 9°13'38.6" N, 79°22'24.7" W, 901 m, 17 Jul 2014, *Batista & Montenegro 1077*, (PMA).

ESCHWEILERA ROSEOCALYX J.E. Bat., S.A. Mori, & J.S. Harrison, **sp. nov.**   TYPE: **Panamá**. Provincia de Panamá, Parque Nacional Chagres, entrando por Altos de Cerro Azul, Cerro Jefe, bosque achaparrado dominado por *Colpothrinax aphanopetala* R. Evans (Arecaceae), 9°13'39" N 79°23'20" W, altura 970 m, 28 Mayo 2016, *J. Batista et al. 1680* (holotype: PMA; isotypes: MO, NY, SCZ, UCH, US). Figures 4–6, 8).

Trees of the understory, 10–12 m tall. **Bark:** outer surface scalloped, grayish-brown, peeling in longitudinal plates, the slash with outer bark thicker than inner bark, the outer bark slash reddish-brown. **Leaves:** petioles 9–20 x 2–6 mm, canaliculate adaxially, blackish when dry; blades elliptic to widely elliptic, sometimes oblong, 20.0–28.2 x 7–13 cm, coriaceous, glabrous, without conspicuous punctuations abaxially, the base rounded, the margins entire, the apex short acuminate; secondary veins in 14–18 pairs, salient abaxially, prominulous adaxially. **Inflorescences:** usually from branches below leaves (ramiflorous), axillary, or terminal (suprafoliar), unbranched to once-branched racemes, the principal rachis 4–8 cm, strongly lenticellate, rough, glabrous; pedicel/hypanthium 5–8 x 3–5 mm, slightly tapered to articulation, lenticellate, glabrous. **Flowers:** 3.5–4.5 cm diam.; hypanthium pinkish, glabrous; calyx lobes 6, widely triangular, 1–4 x 2–5 mm, horizontally oriented at anthesis, the bases not imbricate, fused to one another, pinkish to pinkish-yellow; petals 6, white, 22–40 x 14–24 mm; androecium with ligule 14–25 x 12–23 mm, the hood double-coiled, 15–24 x 16–23 mm, pale yellow; ovary 2-locular, 3–4 ovules per locule. **Fruits:** base conical, 5.7 (including operculum) x 4.5 cm, the pericarp 8–9 mm thick, the calycine ring conspicuous, the infracalycine zone conical, brown, thickened to pedicel/hypanthium the supracalycine zone erect, brown; operculum obconical 2.1 x 4.3 cm. **Seeds:** 3 per fruit, globose, 2–2.3 x 1.3–2 cm; aril spreading (especially along major veins), white.

Ecology and distribution. Understory tree found in cloud forest dominated by *Colpothrinax aphanopetala* R. Evans (Arecaceae) (Fig. 7). It is known from a single tree on Cerro Jefe at 900 to 1000 m in the Chagres National Park (Fig. 8).

Phenology. One collection of flowers has been made in May (*Batista et al. 1680*), and fruiting has been documented in July (*Batista et al. 1682*).

Pollination and dispersal. There are no observations of pollinators visiting the flowers of this species. However, other species of *Eschweilera* have been reported to be pollinated by bees (Gamboa-Gaitán 1997; Mori & Boeke 1987). Likewise, there are no observations of seed dispersal. However, it is likely that the spreading aril surrounding the seeds attracts animals that carry away the seeds to eat the arils.

Etymology. The species epithet refers to the pinkish color of the calyx.

Conservation Status. *Eschweilera roseocalyx* is known from one locality, near the summit of Cerro Jefe. According to IUCN (2012) criteria *E. roseocalyx* is considered Data Deficient (DD).

Discussion. This species is characterized by its small stature; cloud forest habitat; large leaf blade width (over 10 cm wide) which is rounded at the base and short acuminate at the apex; at least some inflorescences ramiflorous; a pinkish hypanthium; broadly triangular calyx-lobes fused to one another at their bases, and pinkish-yellow color when fresh; a double-coiled androecial hood; and an aril that spreads over the entire seed.
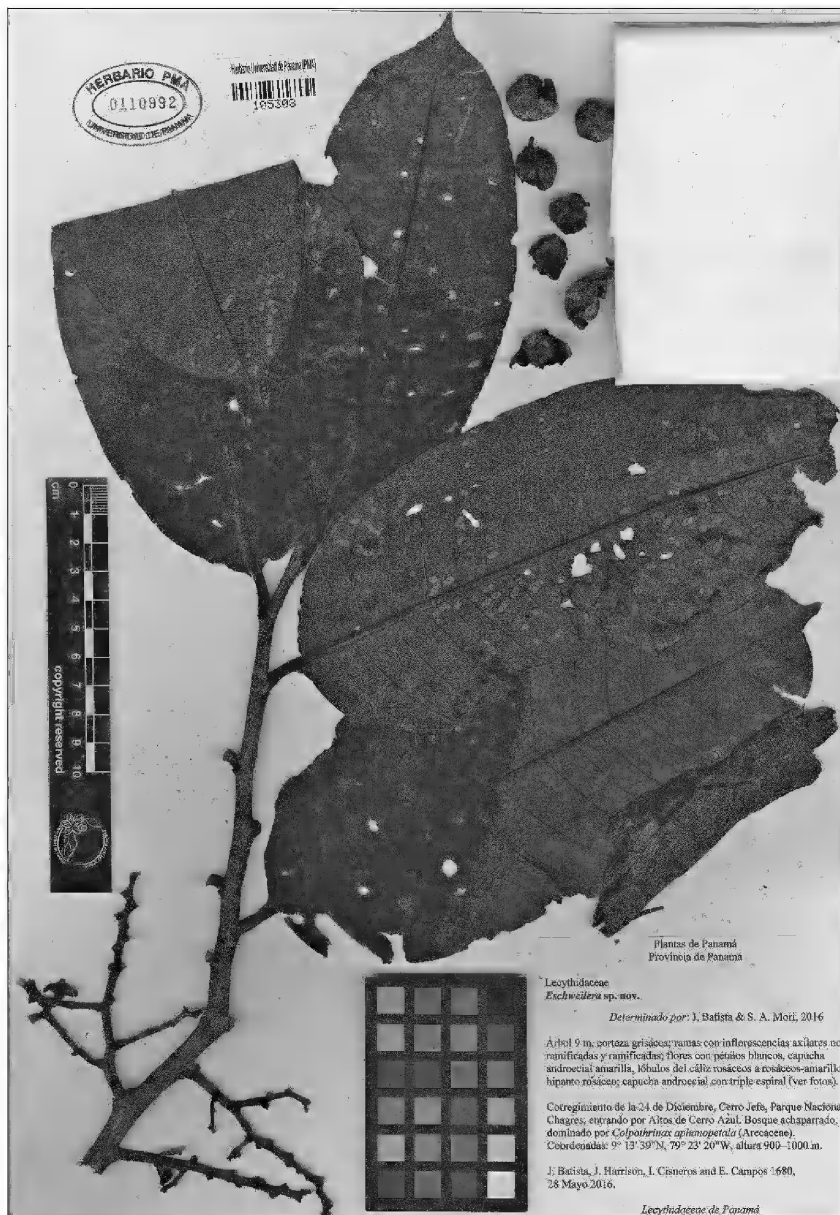
Figure 4. Holotype of *Eschweilera roseocalyx* archived at the University of Panama Herbarium (PMA). Photo by the University of Panama Herbarium.
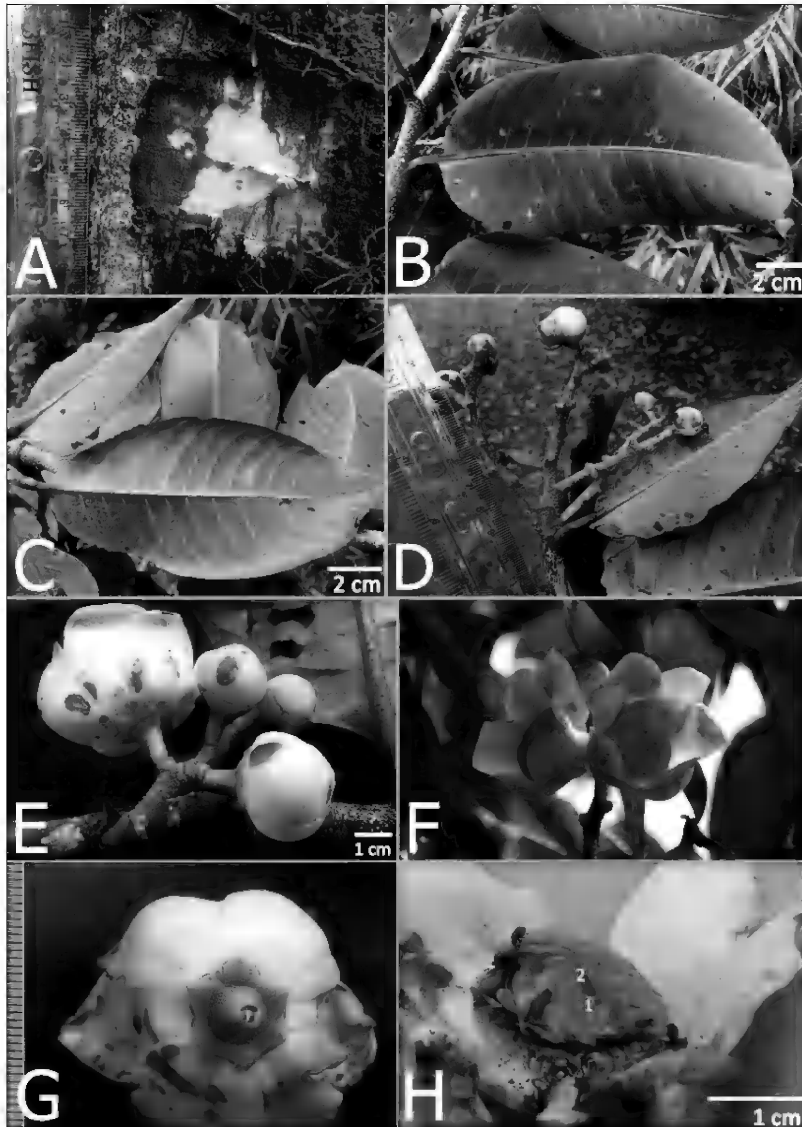
Figure 5. *Eschweilera roseocalyx.* **A.** Grayish-brown outer bark surface and dark reddish-brown slash. **B.** Leaf blade showing adaxial surface. **C.** Leaf blade showing abaxial surface. **D.** Branched inflorescence in bud. **E.** Unbranched inflorescence showing buds and an open flower. **F.** Apical and lateral views of mature flowers. **G.** Basal view of a flower showing white petals, yellow calyx-lobes, and hypanthium. **H.** Medial longitudinal section of an androecial hood showing two coils. Vouchered by J. Batista 1680 [A–H]. Photos by J. Batista [A–D, H] and J. Harrison [E–G].
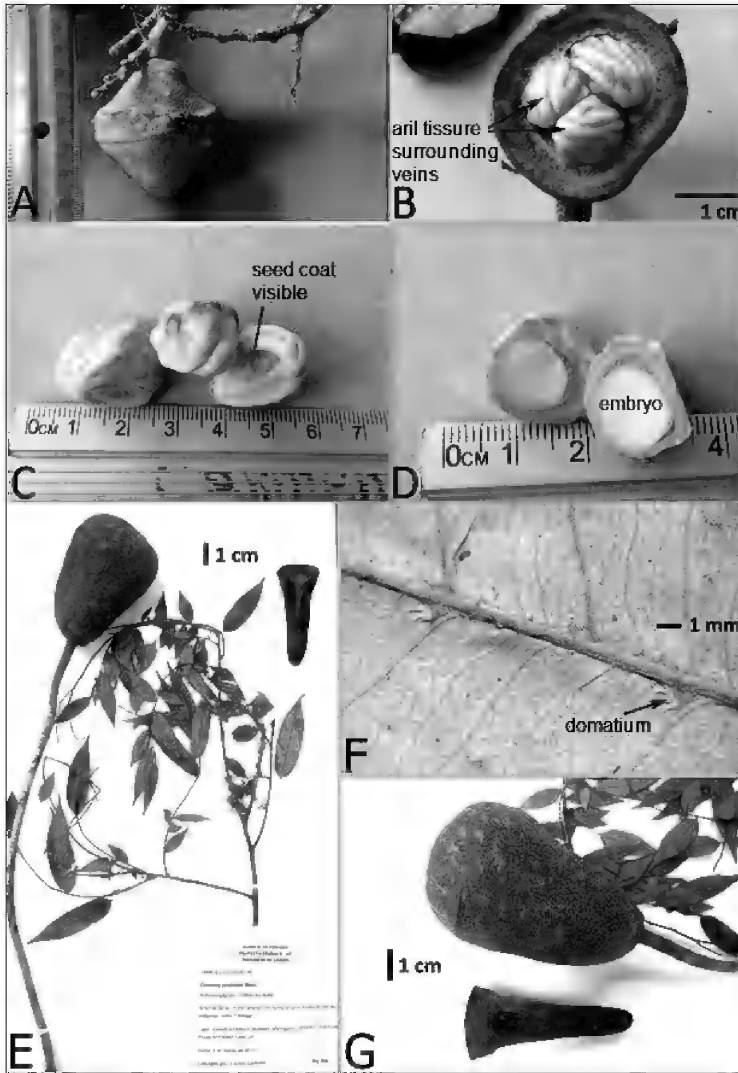
Figure 6. *Eschweilera roseocalyx*. **A**. Immature fruit showing obconical operculum. **B**. Open fruit showing 3 seeds. **C**. Seeds showing aril tissue covering major veins but parts of seed coat between the veins not yet covered by the aril. **D**. Cross-section of a seed showing immature white embryo. Vouchered by *J. Batista et al.* 1682 [A–D]. Photos by J. Harrison [A] and J. Batista [B–D]. *Cariniana pyriformis*. **E**. Fruit collection of *C. pyriformis* at the Universidad de Panamá Herbarium (PMA). **F**. Close-up showing domatia in the axils between the midrib and secondary veins abaxially, note the long, white trichomes along the margin of the domatia. **G**. Pyxidium (fruit) and operculum showing the extended triangular columella. Vouchered by *Garibaldi & Yaleman* 866. Photos by J. Batista.

The *Eschweilera parvifolia* (type of the genus) and *E. integrifolia* clades share the characters of two or three coiled androecial hoods, the presence of vestigial stamen nectaries (also found in species of *Couratari*), ovules in a single row, and lateral arils. They differ, however, in the double-coiled androecial hood of the *E. parvifolia* clade (vs. triple-coiled androecial hood of the *E. integrifolia* clade), and the lateral aril of the *E. parvifolia* clade (vs. the spreading aril of the *E. integrifolia* clade). This species is the first we have seen with a double-coiled androecial hood as found in the *E. parvifolia* clade (Fig. 5H) and a spreading aril as found in the *E. integrifolia* clade (Fig. 6B–D). In short, *E. roseocalyx* could be placed in either clade but this is not surprising because the hood coils are adaptations selected for by pollinators and the aril types are adaptations selected for by dispersal agents (Huang et al. 2015).

The characters that distinguish the *Eschweilera parvifolia* and *E. integrifolia* clades are difficult to score. In the first place, the androecial hood coils are only revealed when the hood is cut in a medial longitudinal section. For example, if a section is not cut through the middle a triple-coiled hood might look like a double-coiled hood but that does not appear to be the case in our section of the androecial hood of *E. roseocalyx* (Fig. 5H), i.e., it is double-coiled. Another problem is that it is difficult to determine when a character state changes enough to be called another character state. In both of these characters the more complicated character states most likely evolved through a continuum of changes. For example, a double-coiled androecial hood and a lateral aril precede the evolution of a triple-coiled androecial hood and a spreading aril, respectively. In *E. roseocalyx* the double-coiled androecial hood (Fig. 5H) and in *E. jefensis* the triple-coiled androecial hood (Fig. 3D) are well defined but it is not always as easy as this to determine the number of coils of some individual. In our definition of androecial hood coils, we do not count vestigial stamen nectaries as a coil.

In the *Eschweilera parvifolia* and *E. integrifolia* clades the funicle is surrounded by an aril. In the least complex type the aril runs laterally along the length of the seed and does not completely cover the seed coat (Type 1). This type of aril is found in the *E. parvifolia* clade (Huang et al. 2015). In a Type 2 aril, tissue spreads from a lateral aril and eventually covers the entire seed coat. Spreading arils do not develop until late in seed development (Fig. 2GH). Thus, in order to describe a spreading aril, the seeds need to be ripe. In addition, the seeds should not be dried until they are studied and photographed because spreading arils dry up and cannot be seen in herbarium specimens. In *E. roseocalyx*, the vascularization of the seed is more complex (Type 3). In this species, the lateral aril splits at the chalazal end of the seed and the proliferation of aril tissue covers all of the major seed veins. The seed coat is mostly covered by aril tissue but some areas of it may not be covered (Fig. 6B–D).

We suggest that *Eschweilera roseocalyx* belongs to the *E. parvifolia* clade because it has a double-coiled, androecial hood. The petals are white and the androecial hood is yellow, a combination of colors that dominates the *E. parvifolia* clade. Nevertheless, some species of the *E. integrifolia* clade have the same flower color (e.g., *E. awaensis* S.A. Mori & Cornejo & *E. collinsii* Pittier). The occurrence of a spreading aril (Type 2) supports the placement of this species in the *E. integrifolia* clade but the Type 3 aril may be different than the Type 2 aril of the *E. integrifolia* clade. Adding this species to a phylogeny based on molecular data should provide insight into the placement of this species.

Additional specimen examined. PANAMA. Provincia de Panamá, Parque Nacional Chagres, entrando por Altos de Cerro Azul, Cerro Jefe, 9°13'39" N, 79°23'20" W, altura 970 m, 26 Jul 2016, *Batista et al. 1682* (NY, PMA, SCZ, UCH).

CARINIANA PYRIFORMIS Miers, Trans. Linn. Soc. London 30: 290, t. 63, figs. 11–13. 1874. TYPE: **Colombia**. Córdoba, Plato Bolivia, Rio Sinu, *Anthoine, s.n. no date* (holotype: K). Miers (1874) interpreted the collecting locality to mean "some small river [called] Betanie flowing into the Magdalena [River] near Plato" in Colombia not Bolivia.

Distribution and Ecology. The nine known species of *Cariniana* (Huang et al. 2008) are found in lowland forests or savanna habitats on well-drained soils. The overall distribution of this clade (see Map 11 in Mori et al. 2017) includes central and southwestern Amazonia, the savanna habitats of central Brazil, and the Atlantic Forest of eastern Brazil. The genus is not known from northern Amazonia and the Guianas. Two species (*C. estrellensis* (Raddi) Kuntze and *C. ianeirensis* R. Knuth) are disjunct between southwestern Amazonia and the Atlantic Forest of eastern Brazil and one species (*C. pyriformis*) is found in lowlands west and north of the Andes in eastern Panama, northern Colombia, and the Maracaibo Basin of Venezuela. Species of *Cariniana* do not occur in dry thorn scrub (= *caatinga*) of northeastern Brazil or in cloud forests.

Conservation status. The World Conservation Monitoring Centre of the IUCN (1998) first classified this species as Lower Risk/Near Threatened (NT) but the IUCN (2001) upgraded the species to Critically Endangered CR A2cd+4cd because of overexploitation of timber and the opening of land for agricultural plantings and for making extensive pastures for livestock grazing (Calderón et al. 2002; Cárdenas & Salinas 2007; Cárdenas et al. 2015).

Cariniana pyriformis is cultivated in botanical gardens in Trinidad, Jamaica, and Singapore (Prance & Mori 1979). Species of *Cariniana* have the best timbers found in Lecythidaceae and wood of *Cariniana pyriformis* has been exported to the United States and Europe under the names of *abarco* (Prance & Mori 1979), *chibugá* (Cárdenas & Salinas 2007), and *Colombian mahagaony* (IUCN 1998) and large stands of this species have been observed in northern Colombia (Record & Hess 1943). Betancur and Raigosa (1973) report that *C. pyriformis* trees are used for reforestation projects in northern Colombia. Because this species is cultivated in plantations and used for forest reclamation projects, it is difficult to determine with certainty if voucher specimens are from native or cultivated trees.

Discussion. Although *Cariniana pyriformis* was suspected to appear in Panama (Mori & Prance 2009) because it has been known from adjacent similar habitats in Colombia since at least 1916 (*H.M. Curran 353*), it was not documented with a herbarium voucher in Panama until 2011 (*Garibaldi & Yaleman 866*).

Specimen examined. Panamá. Provincia de Darién, Comarca Emberá-Wounaan, Marragantí, 8°20'32" N, 77°40'49" W, ca. 66 m, 1 Marzo 2011, *Garibaldi & Yaleman 866* (NY, PMA) (Fig. 6EG).

KEY TO CENTRAL AMERICAN GENERA OF LECYTHIDACEAE
SUBFAM. LECYTHIDOIDEAE

Neotropical Lecythidaceae have flowers and fruits so different from other plant families that special terminology is needed to describe them. In order to understand the terminology consult the online glossary for Lecythidaceae at "The Lecythidaceae Pages" (Mori et al. 2010).

1. Androecium actinomorphic, staminal tube present, androecial hood absent.

    2. Petals 6–8 (–18); stamens 500–1200, the anthers linear, dehiscence poricidal. Fruits usually with 2 or more seeds .... **Gustavia**

    2. Petals 4; stamens 85–210, the anthers globose, dehiscence lateral. Fruits with a single seed .... **Grias cauliflora**

1. Androecium zygomorphic, staminal tube absent (slightly developed in *Cariniana*), androecial hood present (slightly developed in *Cariniana*).

    3. Flower diam. 10 mm or less; androecium forming thin-walled staminal tube, one side of tube slightly elongated. Fruits conical, the pericarp greater than 10 mm thick; seeds with a unilateral wing .... **Cariniana pyriformis**

    3. Flower diam. 10 mm or more; androecial hood well-developed, arising from staminal ring (staminal tube absent). Fruits not conical; seeds without unilateral wings (*Couratari* has circumferential wings).

        4. Inflorescences arising from large tree trunks. Ovaries 6-locular. Fruits cannon-ball shaped, indehiscent; seeds immersed in pulp, the seed coat covered with trichomes .... **Couroupita**

        4. Inflorescences not arising from large tree trunks (a few smaller stature species have cauline inflorescences). Ovaries not consistently 6-locular. Fruits not cannon-ball shaped, usually dehiscent; seeds not immersed in pulp, the seed coats always glabrous.

            5. Androecial hood with external flap, ovary 3-locular. Fruits cylindrical; seeds flattened, with wing encircling margins; cotyledons leaf-like .... **Couratari**

            5. Androecial hood without external flap; ovary usually 2- or 4-locular. Fruits not cylindrical; seeds not flattened; cotyledons absent.

                6. Androecial hoods plane or arched (= not coiled), without vestigial stamen nectaries; ovary usually 4-locular, the ovules in more than 1 row. Seeds with basal arils ...... **Lecythis**

                6. Androecial hoods double- or triple-coiled, with vestigial stamen nectaries at the apices of coils; ovary usually 2-locular, the ovules in a single row. Seeds with lateral or spreading arils .... **Eschweilera**

With the exceptions of *Lecythis* and *Eschweilera*, the Central American genera of Lecythidaceae are monophyletic and will probably retain their current generic status (Huang et al. 2015; Mori et al. 2015). On the other hand, *Lecythis* is not monophyletic. It consists of five clades with three of them native to Central America –– the *Lecythis pisonis* clade (only *L. ampla* Miers), the *L. ollaria* clade (only *L. tuyrana* Pittier), and *L. chartacea* (only *L. mesophylla* S.A. Mori). It is possible that the *L. pisonis* clade will be segregated as a separate genus in the future (Huang et al. 2015; Mori et al. 2017). If that happens, a new generic name for the species of the *Lecythis pisonis* clade will have to be selected, because *Lecythis* Loefl. (Loefling 1758) applies to the *L. ollaria* not the *L. pisonis* clade.

Eschweilera is also not monophyletic. It consists of three clades with two of them, the *Eschweilera parvifolia* and *E. integrifolia* clades, found in both Central and South America. The *E. tetrapetala* clade (Huang et al. 2015; Mori et al. 2017) is limited to the Atlantic Forest and adjacent *cerrado* of Brazil (= savannah). The *E. parvifolia* and *E. integrifolia* clades are morphologically similar clades that have not been retrieved as sister taxa based on molecular data (Huang et al. 2015; Mori et al. 2017). If further molecular study does not show a sister relationship between these two clades then the *E. integrifolia* clade may have to be given a new generic name. If study shows that they are sister to one another, then it would be more appropriate to treat them as subgenera of *Eschweilera*.

Figure 7. Cloud forest habitat of *Eschweilera jefensis* and *Eschweilera rosocalyx* dominated by *Colpothrinax aphanopetala* (Arecaceae). Photo by J. Batista.
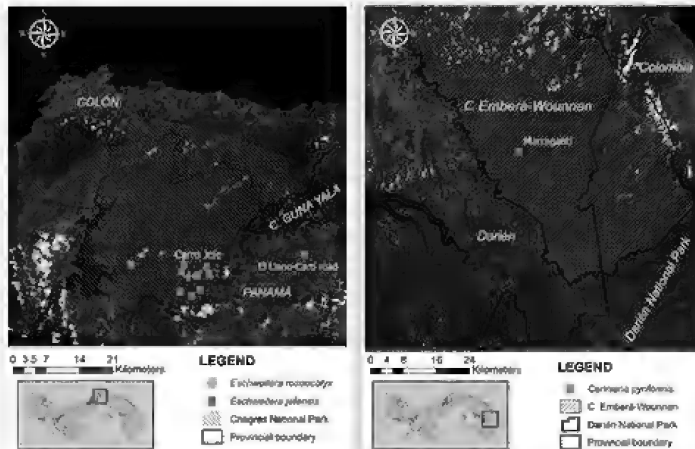

Figure 8. Maps of the Panamanian distributions of *Eschweilera jefensis*, *E. rosocalyx*, and *Cariniana pyriformis*. See Mori et al. (2017) for the overall distribution of *C. pyriformis* in Panama, Colombia, and Venezuela.

ACKNOWLEDGEMENTS

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VALIDATION OF *SELAGINELLA PSITTACORRHYNCHA* (SELAGINELLACEAE), A NEW SPECIES FROM THE GUIANA HIGHLANDS OF VENEZUELA AND BRAZIL

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ABSTRACT

Selaginella psittacorrhyncha Valdespino is validated as a new species from the Guiana Highlands of Venezuela and Brazil by providing a description, illustrations, and discussion on taxonomic affinity, as well as information on conservation status. Its centipede-like habit, ascending to erect stems with anisotomously branching pattern, and strobili born almost laterally on the main stems resemble that of the Panamanian *S. taylorii* Valdespino and *S. chrysoleuca* Spring and *S. euclimax* Alston ex Crabbe & Jermy, both found also in Panama and western South America. *Selaginella psittacorrhyncha* differs from them by its lateral rhizophores, coriaceous leaves, acute and parrot's beak-like median leaf apices, and orange megaspores. *Selaginella psittacorrhyncha* is morphologically closer to *S. vernicosa* Baker of Venezuela and Brazil, from which it is set aside by its ascending to suberect stems, ascending branches, coriaceous leaves, median leaves with the outer bases glabrous or infrequently puberulent only with 1 or 2 short hairs and parrot's beak-like apices.

RESUMEN

Selaginella psittacorrhyncha Valdespino es validada como una especie nueva del Escudo guayanés de Venezuela y Brasil mediante una descripción, ilustraciones y discusión de sus afinidades taxonómicas, así como información sobre su estado de conservación. Su hábito centipediforme, tallos ascendentes a suberectos con un patrón de ramificación anisótomo y estróbilos que se originan casi lateralmente en el tallo principal la asemejan a *S. taylorii* Valdespino de Panamá y a *S. chrysoleuca* Spring y *S. euclimax* Alston ex Crabbe & Jermy, las cuales se encuentran también en dicho país y en el Oeste de Sudamérica. *Selaginella psittacorrhyncha* se diferencia de dichas especies por sus rizóforos laterales, hojas coriáceas y hojas mediales con los ápices agudos, parecidos al pico de un loro y megasporas anaranjadas. *Selaginella psittacorrhyncha* es mucho más cercana morfológicamente a *S. vernicosa* Baker de Venezuela y Brasil, de la que se distingue por sus tallos ascendentes a suberectos, ramas ascendentes y hojas coriáceas, las mediales con los ápices parecidos al pico de un loro.

Selaginella psittacorrhyncha Valdespino was first noticed as an undescribed taxon from the Guiana Highlands in Venezuela and Brazil and included in my previous paper describing some new species from the latter country (Valdespino 2015) as "*S.* sp. A.," with the intended specific epithet "*psittacorrhyncha*." At that time, however, the species could not be formally described because additional studies, including Scanning Electron Microscopy (SEM) of leaves and spores to ascertain morphological features as per Valdespino (2015, 2016, 2017) were underway. Now that such studies are concluded, allowing for a better understanding and documentation of morphological features of the new species as well as a improved assessment of morphologically similar taxa, I formally validate it in accordance with the current ICN (McNeill et al. 2012). Furthermore, this confirms the number of native *Selaginella* species so far found in Brazil to be 80 and the estimated number in Venezuela to be 100, as indicated in Valdespino (2015).

Selaginella psittacorrhyncha somewhat resembles other centipede-like species, including the Panamanian *S. taylorii* Valdespino and *S. chrysoleuca* Spring and *S. euclimax* Alston ex Crabbe &

Jermy, both from Panama and western South America, but it seems morphologically closer to *S. vernicosa* Baker from Mount Roraima, in the state of Bolivar, Venezuela and the state of Roraima, Brazil, in the Guiana Highlands. This region is known for the high diversity and number of endemic *Selaginella* species (Smith 1990; Valdespino 1992; Smith 1995; Valdespino 2016), thus, it is not surprising that new taxa are uncovered as careful specimen examination proceeds.

The description that follows, including measurements data and terminology used to describe leaves and spores, as well as specimens citation and determination of conservation status, was prepared according to Valdespino (2015, 2016, 2017, and references therein). Herbaria acronyms follow Thiers (2017).

SELAGINELLA PSITTACORRHYNCHA Valdespino, **sp. nov.** TYPE: **VENEZUELA**. **Amazonas**. [Depto. Río Negro], Cerro de la Neblina, Río Yatua, 4–8 km SW of Cumbre Camp, 1850–1900 m, 15 Jan 1954, *B. Maguire, J.J. Wurdack, & G.S. Bunting 37298* (holotype: NY; isotype: PMA). Figures 1–4.

Selaginella psittacorrhyncha is morphologically very similar to *S. vernicosa* Baker by its leaf shape but differs noticeably in its ascending to suberect (vs. creeping) habit with the branches ascending (vs. mostly perpendicular to the stem or only slightly ascending), coriaceous (vs. chartaceous) leaves, the lateral leaves on main stem with glabrous (vs. often tufted with 2–6 cilia) basiscopic bases and entire (vs. short-ciliate along proximal ¼–½) basiscopic margins, the median leaves with glabrous or infrequently puberulent only with 1 or 2 short hairs (vs. tufted with 3–5 cilia) outer bases, and distinctly beaked (vs. flat) apices in profile.

Plants terrestrial or epipetric. **Stems** ascending to suberect, stramineous, 6–15 cm long, 0.5–0.7 mm diam., non-articulate, not flagelliform or stoloniferous, 1- or occasionally 2-branched. **Rhizophores** lateral, curving downward as to appear dorsal, borne on proximal ⅕ to ¼ of stems, filiform and stout, 0.1–0.3 mm diam. **Leaves** heteromorphic throughout, coriaceous, strongly imbricate, upper and lower surfaces shiny to waxy and olive colored or on older parts of stems and branches, tawny. **Lateral leaves** imbricate and slightly ascending, ovate-deltate or ovate, 1.8–2.4 × 0.9–1.5 mm; bases truncate, acroscopic bases strongly overlapping stems, basiscopic bases free from stems; acroscopic margins greenish, 1–3 cells wide with the cells elongate, slightly sinuate-walled and glabrous, parallel to margins, shortly-ciliate along proximal ¾ to ⅚ , otherwise entire distally, basiscopic margins greenish, comprising quadrangular, sinuate-walled and glabrous cells, entire or infrequently sparsely and minutely ciliate-denticulate; apices obtuse and entire or infrequently tipped by 1 or 3 teeth; upper surfaces comprising quadrangular, slightly sinuate-walled cells (often difficult to distinguish because of waxy deposits), those along the submarginal to marginal side of basiscopic half and on distal ⅓ of the leaves covered by 1 or 2 papillae, without idioblasts or stomata or with some stomata along basiscopic margin, lower surfaces comprising elongate, sinuate-walled cells, with many of those along distal ⅚ of the leaves covered by 1 or 2 papillae, without idioblast, with 6–8 rows of stomata along midrib. **Median leaves** ascending, broadly deltate-ovate, 0.9–1.4 × 0.6–1.2 mm; bases truncate, the outer base glabrous or infrequently puberulent with 1 or 2 short hairs, without auricles; margins greenish, 1–3 cells wide with the cells elongate, slightly sinuate-walled and glabrous, parallel to margins, shortly-ciliate along proximal ⅞, otherwise entire distally; apices acute, prominent and beaked, tipped by an often caducous short cilium or teeth-like projection; both surfaces without conspicuous idioblasts, upper surfaces comprising quadrangular, slightly sinuate-walled cells (often difficult to distinguish because of waxy deposits), those along the submarginal to marginal side of basiscopic half and on distal ⅔ of the leaves covered by 1 or 2 papillae, without idioblasts, with stomata in 3–5 rows along distal ⅔ of the midribs, lower surfaces comprising elongate, sinuate-walled cells, without stomata. **Axillary leaves** ovate to ovate-oblong or similar to lateral leaves, 1.8–2.0 × 1.0–1.3 mm; the bases, margins, apices, and surfaces as in lateral leaves. **Strobili** terminal on main stem and branch tips, quadrangular, 0.4–5.5 cm. **Sporophylls** monomorphic, without a laminar flap,

Figure 1.　*Selaginella psittacorhyncha*, sp. nov. (*Maguire et al. 37298*, holotype, NY).
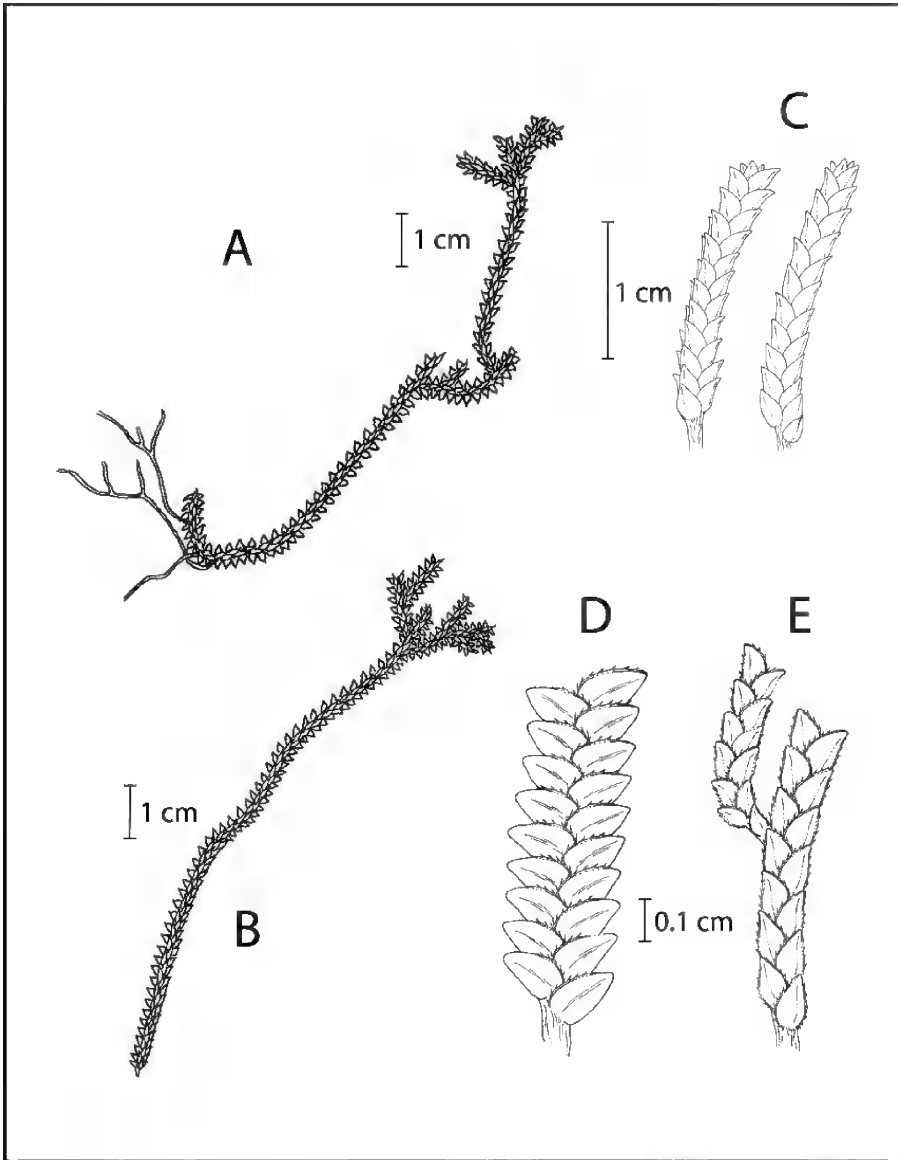
Figure 2.   *Selaginella psittacorhyncha* sp. nov.   **A–B**. (*Maguire et al. 27823,* paratype, NY); **C–E** (*Maguire et al. 37298,* holotype, NY). **A–B**. Habit. **C**. Strobili. **D**. Close-up of lower surface of stem section showing lateral leaves. **E**. Close-up of upper surface of stem section showing median leaves. Illustration made by Rubén Lozano.
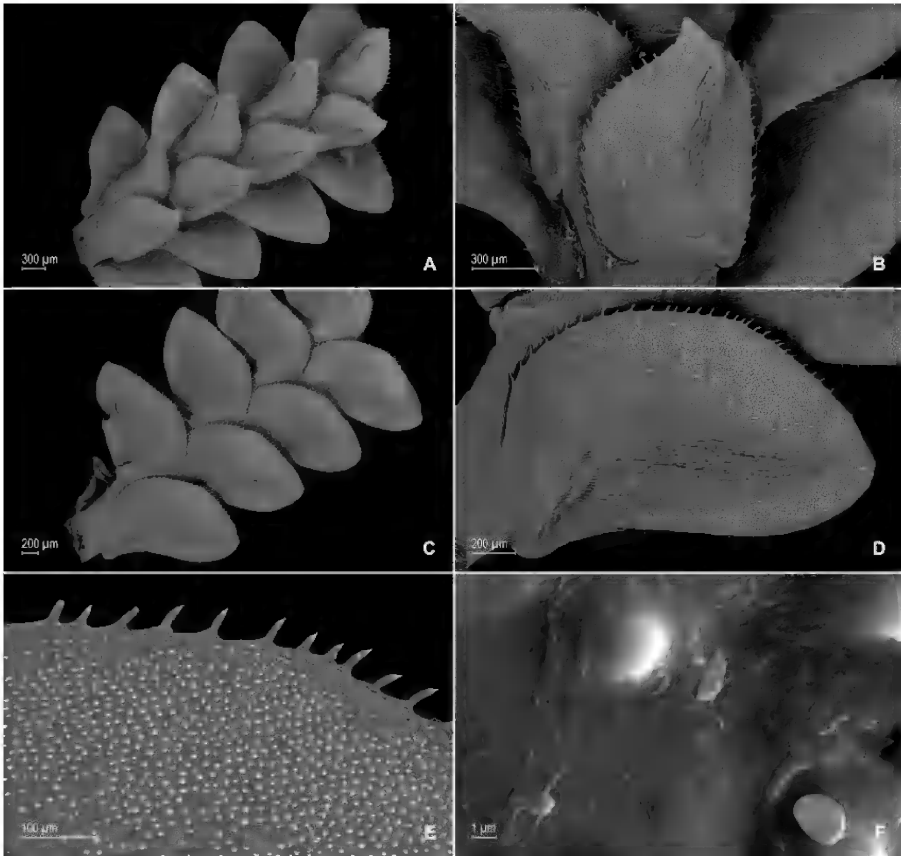
Figure 3.   SEM micrographs of branch sections and leaves of *Selaginella psittacorhyncha* sp. nov. (*Maguire et al. 37298*, holotype, NY). **A**. Section of upper surface of stem. **B**. Upper surface of median leaf. **C**. Section of lower surface of stem. **D**. Lower surface of lateral leaf. **E**. Detail section, acroscopic margin of lateral leaf lower surface. **F**. Close-up of lower surface of lateral leaf; note papilla.

each with a strongly developed and seemingly glabrous keel along midribs often ending in a single short cilium or teeth-like projection, broadly ovate to ovate-deltate, 1.5–1.8 × 0.9–1.5 mm; bases rounded to truncate; margins as in median leaves; apices acute to obtuse, often beaked, tipped by 1–3 short cilia or teeth-like projections; **dorsal sporophylls** with upper and lower surfaces as in vegetative leaves; **ventral sporophylls** with both surfaces of the same color as the vegetative leaves, comprising elongate, sinuate-walled cells on both surfaces.   **Megasporangia** in 2 ventral rows and often on distal ½ of 2 dorsal rows; **megaspores** deep orange, rugulate-reticulate on proximal faces with verrucate and perforate microstructure, rugulate-reticulate on distal faces with reticula formed by very low muri and granulate and perforate microstructure (Figure 4C & D), 355–375 µm. **Microsporangia** in 2 dorsal rows or only on proximal ½ of 2 dorsal rows; **microspores** deep orange, gemmate on proximal and distal faces with psilate microstructure (Figure 4E & F), 50–58 µm.

Habitat and Distribution. *Selaginella psittacorrhyncha* grows in or around rocky cliffs in montane highland savannas, on wet ledges of cliffs in scrub forests, sandstone outcrops above swampy savanna or on bare earth at base of grass tussocks at 1600–2343 meters; it is documented here in Cerro Sipapo, Venezuela, and Cerro de la Neblina in both Venezuela and Brazil.

Etymology. The specific epithet derives from the Latin "*psittacus*," meaning parrot, and "*rhynchus*," nose; together these allude to the median leaf apices resembling a parrot's beak.
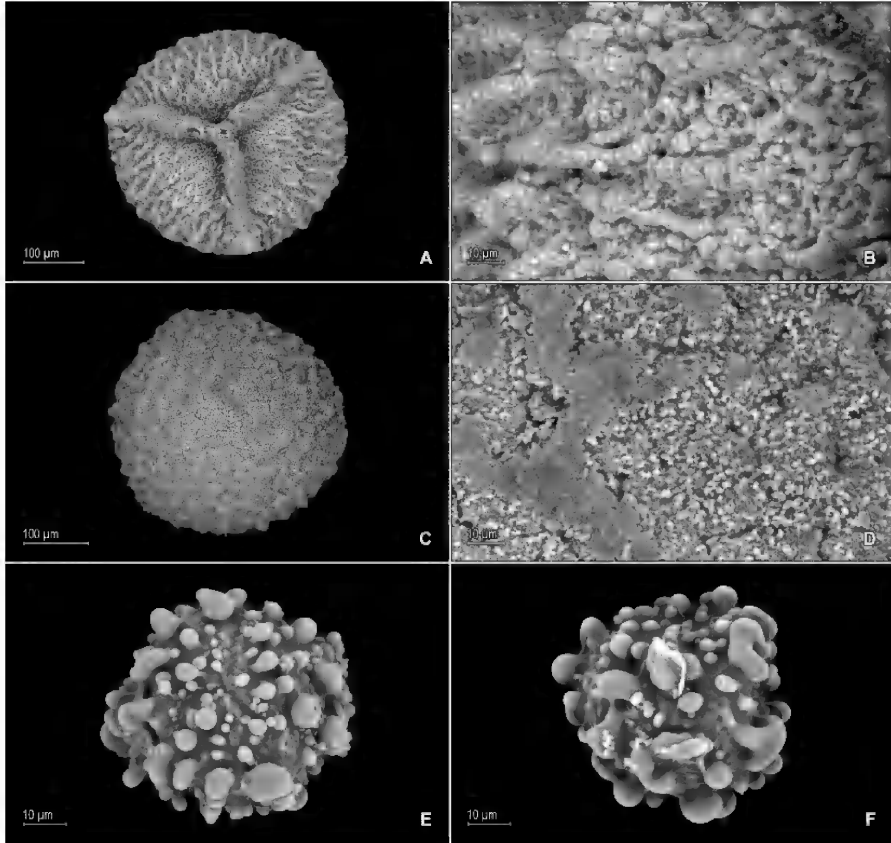
Figure 4.   SEM micrographs of spores of *Selaginella psittacorhyncha* sp. nov. (*Maguire et al. 37298*, holotype, NY). **A**. Megaspore, proximal face. **B**. Close-up of megaspore, proximal face. **C**. Megaspore, distal face. **D**. Close-up of megaspore, distal face. **E**. Microspore, proximal face. **F**. Microspore, distal face.

Conservation status. *Selaginella psittacorrhyncha* is here documented in two distinctly isolated tepuis at high elevations in the Amazon basin of Venezuela and Brazil. These areas are difficult to reach by humans and, therefore, the species may not face imminent anthropomorphic-based threats. Accordingly, I tentatively consider it of Least Concern (LC) according to IUCN categories and criteria (2012).

Additional specimens examined (paratypes): **VENEZUELA**. Amazonas. Cerro Sipapo (Paráque), west Peak, 1600 m, 20 Dec 1948, *Maguire & Politi 27823* (NY); [Depto. Río Negro], Cerro de la Neblina, Río Yatua, Cañon Grande basin, 1200–2200 m, 15 Dec 1957, *Maguire et al. 42417* (NY, PMA), Venezuelan-Brazilian Frontier, Neblina Massif, Camp 12, 1950 m, 26–27 Feb 1985, *Boom et al. 6013* (NY, PMA), Cerro de la Neblina, Planicie de Zuluaga, Río Titirico, 2300 m, 10–15 Oct 1970, *Steyermark 103899* (NY), vicinity of Camp VI, on a ridge on Venezuelan-Brazilian border [Cerro de la Neblina], 3.5 km W of Pico Zuloaga, 00°53'N, 65°56'W, 2000 m, 13–15 Apr 1984, *Thomas & Plowman 3145* (NY). **BRAZIL**. Amazonas: São Gabriel da Cachoeira, Parque Nacional do Pico da Neblina, trilha para cachoeira do Anta, Alto da Serra da Neblina, acampamento do Marco 5 da fronteira do Brasil com a Venezuela, 00°48'57"N, 65°58'06"W, 2343 m, 31 Dec 2004, *Carvalho et al. 374* (INPA n.v., PMA).

Selaginella psittacorhyncha is characterized by its centipede-like habit, ascending to erect stems that branch anisotomously once or twice. The secondary branches ascending and striplike or ribbon-shaped, rhizophores borne laterally on stems (a feature that to my knowledge has not been reported before in the genus) that curve downward as to appear dorsal in position, coriaceous leaves, strongly beaked median leaf apices, and orange megaspores. Its overall habit, branching pattern, and strobili position are reminiscent of those found in *S. chrysoleuca*, *S. euclimax*, and *S. taylorii*. Nevertheless, *S. psittacorrhyncha* differs from those species by its lateral rhizophores, coriaceous leaves, acute and parrot's beak-like median leaf apices, and orange megaspores. As previously mentioned, a closer morphological allied species of *S. psittacorrhyncha* is *S. vernicosa* but the former is most distinct by the characters discussed under the diagnosis. In addition, *S. psittacorhyncha* is known from the tepuis of Cerro de la Neblina and Cerro Sipapo, whereas *S. vernicosa* is only known from Mount Roraima in Venezuela and Brazil.

ACKNOWLEDGEMENTS

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OCCURRENCE OF *SOLIDAGO CANADENSIS* VAR. *HARGERI* IN TENNESSEE

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ABSTRACT

Fernald recognized *Solidago canadensis* var. *hargeri* in 1915 and gave its range as mostly in the New England area. By the time the 8th edition of Gray's Manual was published, he had extended the range to Tennessee, but subsequent workers concerned with the Tennessee flora have never mentioned this taxon. A collection by Gattinger in the Gray Herbarium and additional collections and chromosome counts provided here support the inclusion of *S. canadensis* var. *hargeri* as part of the Tennessee flora.

The *Solidago canadensis* L. complex is one of the most confusing complexes in *Solidago*. Most of the treatments of this complex have been by botanists in the Midwest, Northeast, and adjacent Canada, where this complex is well developed and its members are hard to separate. The complex is not as confusing in Tennessee once *S. gigantea* Ait. and *S. rupestris* Raf. are separated out. The remaining plants have traditionally been treated as a single species, but Fernald (1950) indicated that both *S. altissima* L. and *S. canadensis* var. *hargeri* Fern. occur in Tennessee. Croat (1972) also gives Tennessee for his range of var. *hargeri*, presumably copying Fernald's range in Gray's Manual. Other authors dealing with the flora of Tennessee have never mentioned var. *hargeri*.

Melville and Morton (1982) treated the *Solidago canadensis* complex in Ontario, concluding, using breeding studies, chromosome counts, and morphology, that both *S. altissima* and *S. canadensis* var. *hargeri* should be considered good taxa in Ontario. This paper and the earlier one by Croat probably convinced Cronquist (1991) to finally accept var. *hargeri*. He still considered *S. altissima* best treated as *S. canadensis* var. *scabra* Torr. & Gray but did not give a separate range for each of the varieties. Semple and Cook (2006) accepted both *S. altissima* and *S. canadensis* var. *hargeri*, with the range for var. *hargeri* only extending into Kentucky. By the time their treatment was published, chromosome numbers for each taxon were known –– *Solidago altissima* is either tetraploid ($2n = 36$) or hexaploid ($2n = 54$), while *S. canadensis* var. *hargeri* is diploid ($2n = 18$). A multivariate morphometric study by Semple et al. (2015) of the *S. altissima* complex and *S. canadensis* further supports the acceptance of var. *hargeri*. However, they point out the problem of separating some specimens of var. *hargeri* from *S. altissima* var. *gilvocanescens* (Rydb.) Semple where the ranges overlap. The var. *gilvocanescens*, mostly from the Great Plains, is not found in Tennessee. Throughout this time, publications dealing with the flora of Tennessee, such as the most recently published Guide to the Vascular Plants of Tennessee (2014), only considered *S. altissima* (synonym = *S. canadensis* var. *scabra*) as occurring in Tennessee.

The Gray Herbarium staff was kind enough to verify that a specimen there annotated as var. *hargeri* from Tennessee was collected by Gattinger in Nashville. Additional collections and chromosome counts by the author also support the occurrence of var. *hargeri* in Tennessee. The Tennessee counties where *S. canadensis* var. *hargeri* has been found are all close to Kentucky and make the Tennessee sites a reasonable range extension.

The following chromosome counts and specimens document *S. canadensis* var. *hargeri* as part of the flora of Tennessee.

Chromosome counts of $n = 9_{II}$

Tennessee. Claiborne Co.: Tazewell, moist field next to creek, 15 Aug 1968, *Morton 2925, 2926A&B,* and *2926-1A&B* (NY).

Herbarium specimens

Tennessee. Claiborne Co.: Tazewell, moist field next to creek, 15 Aug 1968, *Morton 2924* (NY); Tazewell, moist field along Russell Creek, 16 Aug 2016, *Morton 9491* (TENN, UCHT); Davidson Co.: Nashville, 1885, *Gattinger* (GH).

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OVERVIEW OF *POTENTILLA VERSICOLOR* (ROSACEAE)
AND A NEW VARIETY
IN THE "SKY ISLANDS" OF CENTRAL AND EASTERN OREGON

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ABSTRACT
Potentilla versicolor Rydb. was resurrected for use in *Flora of North America North of Mexico* for a plant variously included in *P. ovina, P. breweri,* or *P. millefolia.* Because of the poorly known status of a species of possible conservation concern, discussion beyond what has previously been published, including infraspecific variation, is provided here. As treated in FNANM, the species comprises pinnate-leaved, sparsely to non-tomentose *Potentilla* occurring on "sky islands" in central and eastern Oregon and northern Nevada, specifically Gearhart, Steens, Greenhorn, Strawberry, Wallowa, and eastern Cascade mountains of Oregon, and the Ruby Mountains of Nevada. Populations from ultramafic substrates in the Greenhorn and Strawberry mountains tend to have more leaflets, more diffuse inflorescences, and smaller flowers than elsewhere; they are described here as **Potentilla versicolor** var. **darrachii** Ertter & DiNicola, **var. nov.** Other infraspecific variation in the species is currently under investigation by the second author.

As the first continent-wide revision of *Potentilla* since Rydberg (1908), the treatment of the genus in *Flora of North America North of Mexico* (FNANM) by Ertter et al. (2015) frequently diverged from previous treatments in available regional floras (e.g., Abrams 1944; Cronquist et al. 1997; Hitchcock et al. 1961), most of which differ among themselves in various details. As a prime example, the FNANM treatment resurrected *P. versicolor* Rydb. for pinnate-leaved, sparsely or non-tomentose *Potentilla* from high-montane settings in the northern Intermountain Region, specifically from central and northeastern Oregon and northern Nevada. Because this previously overlooked and relatively rare species was only cursorily addressed in the FNANM format, a more detailed discussion is provided here, including the description of a new ultramafic-associated variety. Additional information on related species is in a recent companion paper (Ertter 2017); the species complex as a whole is currently under investigation as the second author's doctoral study.

Rydberg (1908) described *Potentilla versicolor* based on a single collection from central Oregon, collected in 1896 by F.V. Coville (*#307*, US) and J.B. Leiberg (*#2918*, ORE in OSC) from "Grayhart Buttes" ("Gayhart" on *Leiberg 2918*), generally understood to be Gearhart Mountain in Lake County, Oregon. No subsequent collections were added to the circumscription for over half a century. Few floras have covered this part of Oregon, a primary exception being that of Abrams

(1944), who dismissed *P. versicolor* as "doubtful, for it is known from a single collection." Keck (in Clausen et al. 1940) treated *P. versicolor* as a variant of *P. breweri* S. Wats. with "leaflets small and rather well separated." Peck's *A Manual of the Higher Plants of Oregon* was the first (and for decades the only) flora to recognize *P. versicolor*, initially limited to "mountains of southern Lake Co." (Peck 1941), but with the range subsequently expanded to include the Wallowa and Steens mountains (Peck 1961). With the exception of Mansfield's (2000) *Flora of Steens Mountain* (which was influenced by the manuscript for Ertter et al. 2015), other treatments have variously relegated the name and/or specimens to *P. breweri*, *P. ovina* J.M. Macoun (e.g., Hitchcock et al. 1961), or *P. millefolia* Rydb. (e.g., Johnston 1980; Cronquist et al. 1997).

The recognition and circumscription of *Potentilla versicolor* in FNANM resulted from herbarium studies, fieldwork, and common garden observations over the last several decades, which have confirmed that plants comparable to the type of *Potentilla versicolor* form reasonably uniform populations at high elevations in the scattered "sky island" system of eastern Oregon, specifically Steens Mountain, Gearhart Mountain, the Wallowa Mountains, the Greenhorn Mountains, and the Strawberry Mountains, from 2100 to 3200 meters elevation. Some populations from the northern Ruby Mountains of northern Nevada also fit morphologically within *P. versicolor*, as do some populations from the eastern Cascade Mountains (e.g., the Sky Lakes Wilderness area). Occurrences often show intergradation with co-occurring populations of *P. breweri* and other species, but relatively "pure" subpopulations indicate that *P. versicolor* is as distinct as any other species in *Potentilla* sect. *Multijugae* (Rydb.) A. Nelson.

As now circumscribed, *Potentilla versicolor* is distinguished by its somewhat thickened taproot, simple to few-branched caudex, prostrate to ascending stems that are usually more than 1.5 times as long as the leaves, pinnate leaves with confluent terminal leaflets, usually sparse to absent vestiture (more variable on Gearhart Mountain), and a diffuse inflorescence with relatively straight pedicels. Leaflets are palmately and deeply divided into narrowly elliptic or linear-lanceolate teeth or segments, which when fresh appear semiverticillate (Fig. 1). Intertwined cottony hairs are usually absent or sparse, with the latter state possibly resulting from intergradation with co-occurring *P. breweri*. Petals, filaments, and styles tend to be somewhat shorter in *P. versicolor* than in *P. breweri*. Vigorous populations are most often found on shallow rocky soils, often near outcrops and/or with abundant cobble-size rocks, which are moist early in the season but dry out as the season progresses.

Figure 1. Semiverticillate leaf of *Potentilla versicolor* var. *versicolor* on Steens Mountain. Photo by B. Ertter.

A key to distinguish *Potentilla versicolor* from the species with which it is most often conflated, and including the new variety described below, is as follows (modified from Ertter et al. 2015, with characters as defined therein). See discussion for plants from Ruby Mountains, Nevada.

1. At least distal leaflets pinnately incised, all leaflets ± distinct; often on calcareous substrates, primarily Rocky Mountains and eastern Great Basin ranges (confirmed in Oregon only from high peaks in the Wallowa Mountains) .... **Potentilla ovina**
1. Leaflets ± palmately or unevenly incised (pinnately in rare exceptions), distal leaflets ± confluent; rarely if ever on calcareous substrates, Oregon, Nevada, and California.

　2. Pedicels ± recurved in fruit; stems usually prostrate, 1–2 times as long as basal leaves; meadows in shrub-steppe and low- to mid-montane forest communities (700–2200 m), ne California, s-central Oregon, adjacent Nevada .... **Potentilla millefolia**
　2. Pedicels straight to slightly recurved in fruit; stems prostrate to ascending, 2–3(–7) times as long as basal leaves; various habitats in mid-montane conifer forests to alpine fell-fields (1500–3600 m).

　　3. Leaflets grayish green to white with ± dense cottony hairs, straight hairs usually obscured or absent; caudex commonly branched; filaments (1–)2–4 mm long; high Sierra Nevada and mountains of n California, Oregon, and n Nevada .... **Potentilla breweri**
　　3. Leaflets usually green to grayish green with sparse (to common on Gearhart Mountain) or absent cottony hairs, straight hairs sometimes abundant (primarily on emerging leaves); caudex usually simple to few-branched; filaments 1.5–2.5(–3) mm long; mountains of Oregon .... **Potentilla versicolor**

　　4. Inflorescence branch angle 30–70(–90)°; pedicels to 2.5(–3.5) cm long; leaflets 3–6(–10) per side on distal ± ½(–¾) of leaf-axis; salient glandular trichomes present or absent, cottony hairs usually absent or sparse; basaltic, metamorphic (but not ultramafic), and granitic substrates; Steens, Gearhart, Wallowa, and Cascade mountains .... **var. versicolor**
　　4. Inflorescence branch angle 60–100°; pedicels to 3.5(–4) cm long; leaflets (5–)6–9 per side on distal (½–)⅔–¾ or more of leaf-axis; salient glandular trichomes present, cottony hairs always absent; ultramafic substrates; Strawberry and Greenhorn mountains .. **var. darrachii**

Variation within *Potentilla versicolor*

　　Noteworthy variation occurs from mountain range to mountain range within the distribution of *Potentilla versicolor*, suggesting that the species has undergone radiation in the "sky islands" of the northern Great Basin. The second author is currently investigating this hypothesis, along with the possible contribution of introgression with *P. breweri* and other co-occurring congeners. Distinctions noted to date among metapopulations include the following.

　　(1) The type of *Potentilla versicolor* and recent collections by the second author from Gearhart Mountain approach *P. breweri* in having more cottony late-season leaves than most other populations. Styles are exceptionally long and slender as well, and less likely to stay attached to the achenes. At least one collection in the relatively nearby Cascade Mountains (*Dennis 2861*, OSU) is morphologically comparable. All known populations are on basaltic substrates.

　　(2) Steens Mountain in Harney County, Oregon, supports the largest and most accessible metapopulation of *Potentilla versicolor* by far, with numerous occurrences throughout the treeless upper expanses from at least 2530 to 2900 m elevation, on basaltic substrates. Because of the relative abundance of available material, collections from Steens Mountain are the primary basis for the description of *P. versicolor* in FNANM, supplemented with specimens from other sites. Existing collections have mostly been identified as either *P. breweri* or *P. ovina* using standard regional floras (Cronquist et al. 1997, Hitchcock et al. 1961, Hitchcock & Cronquist 1973). *Potentilla breweri* is

also present on Steens Mountain, evidently hybridizing with *P. versicolor,* but *P. ovina* is now treated as a more eastern species confirmed in Oregon only from high peaks in the Wallowa Mountains (Ertter et al. 2015).

(3) Collections of *Potentilla versicolor* from metamorphic and granitic substrates in the Wallowa Mountains (referred to as the "Powder River Mountains" on some older labels) are most comparable to those from Steens Mountain, though the leaves tend to have more leaflets occupying more of the leaf-axis. Although some collections were provisionally annotated by the senior author as var. *darrachii,* subsequent research indicates that optimum placement of the Wallowa Mountains metapopulation remains to be determined. Putative hybridization with co-occurring *P. glaucophylla* Lehm. has resulted in significant variation, some of which might represent a semi-stabilized nascent taxon.

(4) Metapopulations from ultramafic substrates in the Greenhorn Range of the Blue Mountains and Strawberry Mountains of Oregon are described below as var. *darrachii.*

(5) Several collections from Island Lake and Liberty Pass in the Ruby Mountains of Elko County, Nevada, have a strong resemblance to *Potentilla versicolor* in Oregon, particularly to the Steens Mountain form. Whether these are conspecific or have an independent origin, possibly involving *P. ovina*, remains to be determined.

(6) The first author had previously included some collections (*Thompson 13225, Applegate 7535*) from Crane Mountain, Lake County, Oregon, within *Potentilla versicolor* and annotated them accordingly. More recent fieldwork, however, indicates that they are more likely variants, or even possible topotypes, of *P. bruceae* Rydb.

(7) Even in the broad sense, *Potentilla versicolor* is not currently recognized in California (Ertter 2012; Ertter et al. 2015), but the type of *P. millefolia* var. *algida* Jepson has tantalized the first author for some years with its similarities to *P. versicolor* (e.g., Ertter & Mansfield 2007). Jepson (1936) based this variety on a single collection (*Hall 8698,* UC) from a glacial meadow at the head of the North Fork of Swift Creek in the eastern Salmon Mountains of Trinity County, California. Some recent collections from the Mount Eddy area by the second author are comparable to the type, but other populations from ultramafic substrates in the Scott and Trinity mountains, and possibly Mount Shasta, are consistently intermediate between *P. breweri* and *P. versicolor.*

A new variety of *Potentilla versicolor*

While working on the treatment for FNANM, the first author was puzzled by a specimen from the Greenhorn Range in the Blue Mountains of Oregon, collected by Jean Wood in 2002 as part of a floristic survey of the Umatilla National Forest. With the help of forest botanist Mark Darrach, this population was relocated in 2012; two years later Darrach found another population nearby. Comparable plants on Baldy Mountain in the Strawberry Mountains had been photographed by Paul Slichter in 2010 and were brought to the authors' attention in 2015. Both sites found by Slichter were visited by the authors later that same year, shortly before a major forest fire burned through the area.

Plants from both the Greenhorn and Strawberry mountains clearly belong to *Potentilla versicolor* sensu lato, but they have a generally greener and more delicate gestalt, more leaflets on average, more diffuse inflorescences, and smaller flowers, especially compared to populations from Steens Mountain. These metapopulations also are restricted to ultramafic substrates, commonly associated with unique species and varieties of plants in other areas. Although the morphological distinctions were diminished in plants grown in a common-garden setting with regular watering, sufficient differences persisted to support the recognition of these populations as a definable variety on ultramafic substrates in contiguous parts of the species' range, as described here.

POTENTILLA VERSICOLOR Rydb. var. DARRACHII Ertter & DiNicola, **var. nov.**   (Figures 2, 3). TYPE: **USA. Oregon.** Grant Co.: head of Salmon Creek on NE side of Vinegar Hill, Blue Mts. ca 28 air mi NE of John Day, open conifer forest on serpentine, 2280 m, 44.717°N 118.551°W, 3 Aug 2012, *B. Ertter 21219* with M. Darrach & E. George (holotype: UC; isotypes: CIC, MO, NY, OSC, PR, RM, SRP, US, WIS, WTU, and to be determined.)

Differs from var. *versicolor* (particularly on Steens Mountain) in generally having more leaflets per side on a greater fraction of the relatively slender leaf-axis, a more openly branched inflorescence with longer pedicels on average, fewer and slightly smaller flowers, fewer carpels, styles that are smooth rather than somewhat swollen-papillate basally, and an association with ultramafic substrates.

Plants usually green, sometimes grayish green in late season; taproot not to somewhat fleshy-thickened; caudex simple to few-branched. **Stems** prostrate-decumbent in open sites, ascending in competing vegetation, (0.8–)1–3(–3.5) dm long, 1.5–2.5(–7) times as long as basal leaves. **Basal leaves** not evidently 2-ranked, pinnate with distalmost leaflets ± confluent, (2–)4–10(–15) × (0.6–)0.8–2(–3.5) cm; petiole (0.5–)1–2.5(–4.5) cm long, glabrous (early season) to sparsely (late season) wavy-hairy, often sparsely glandular as well; leaflets (5–)6–9 per side, on distal (½–)⅔–¾+ of leaf-axis, overlapping at least distally, largest leaflets cuneate to flabellate, (0.3–)0.7–1.2(–2) × (0.2–)0.4–1.0(–1.5) cm, palmately divided (½–)⅔ to completely to midrib, often medially split, ultimate teeth or segments 2–4(–6) in a semiverticillate arrangement, narrowly elliptic to linear-oblanceolate, rarely obovate, (1–)2–8(–12) × 0.5–2(–4) mm, surfaces similar, green (grayish) with sparse (especially early season) to common (primarily late season) straight to ± wavy hairs, these weak, ascending, 0.5–2 mm long, salient peglike glands sparse to common, often pink-headed, cottony hairs absent. **Cauline leaves** (0–)1(–3). **Inflorescences** (1–)3–10(–12 or more in cultivation)-flowered, very openly cymose; inflorescence branch angles 60–100°; pedicels (1–)2–3.5(–4) cm long, straight to slightly recurved in fruit. **Flowers**: hypanthium 3–4 mm diam., epicalyx bractlets lanceolate to ovate-elliptic, 2–3.5 × ± 1 mm; sepals 3.5–5 mm long, narrowly to broadly acute; petals yellow, lacking darker basal patch, 5–7 × 4–5 mm; filaments 1.5–3 mm long; anthers 0.7–0.8(–1) mm long; carpels 5–15, styles slender, 2–2.5 mm long, smooth at base. **Achenes** ± 1.8 mm, smooth, pale brown.

Flowering June to August. Moist ground along drainages in open conifer forests near timberline, sometimes in rock crevices, on ultramafic substrates; 2000–2400 m.

Additional specimens examined. Oregon. Grant Co.: Salmon Creek watershed, Vinegar Hill RNA, Greenhorn Mts., 8 Jul 2014, *Darrach 1070* (CIC); Pine Creek trail up N side of Baldy Mt., Strawberry Range ca 8 airmi SE of John Day, 44.347°N 118.8045°W, 2026 m, 13 Jun 2015, *Ertter & DiNicola 22341* (OSC, SRP, UC, WIS, and to be determined); saddle between peaks of Baldy Mt. (= serpentine ridge) in Strawberry Range ca 9 airmi SE of John Day, 44.3311°N 118.7912°W, 2165 m, 13 Jun 2015, *Ertter & DiNicola 22357* (CIC, OSC, UC, WIS, and to be determined); Salmon Creek below Bimetallic Mine, ca ¾ airmi E of Vinegar Hill Peak, T10S R35E S7, 7000 ft, 10 Jul 2002, *Wood 7784* (RM, Umatilla NF herb.).

As currently understood, *Potentilla versicolor* var. *darrachii* is known from two metapopulations in the mountains of northeastern Oregon, each with two known occurrences: the Greenhorn Range of the Blue Mountains, and Baldy Mountain in the Strawberry Mountains. Plants grow on ultramafic substrates in moist ground at the edge of rocky drainages in open conifer forests near treeline.
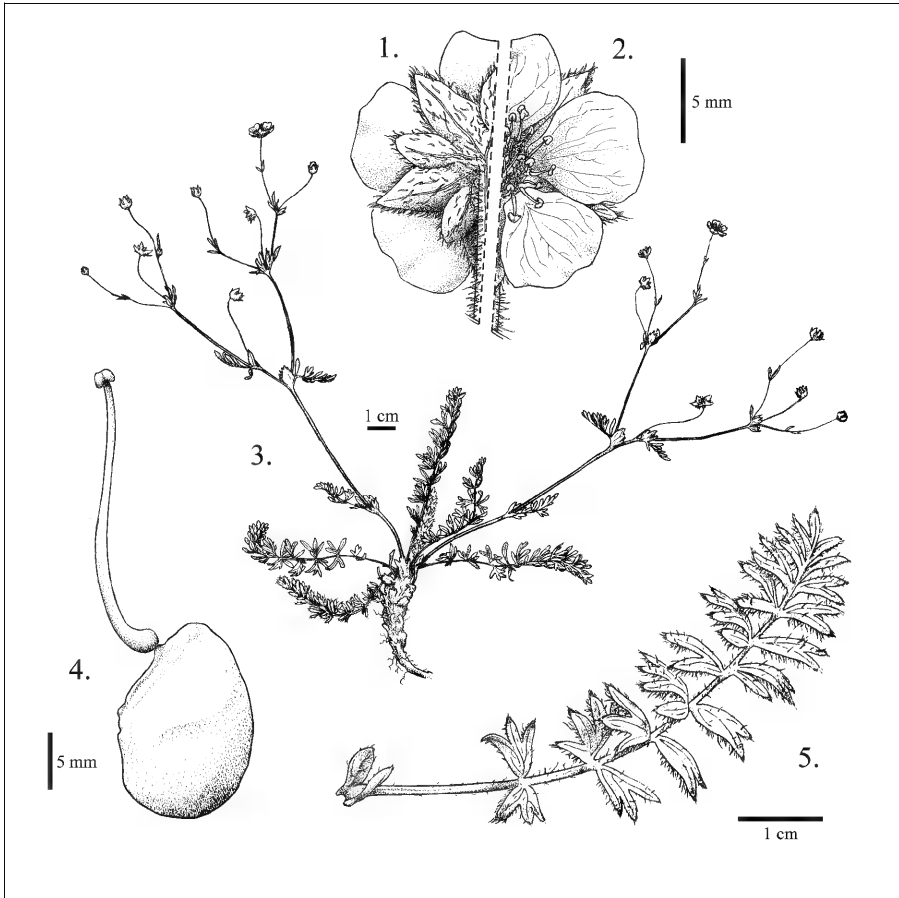
Figure 2. *Potentilla versicolor* var. *darrachii* Ertter & DiNicola. 1. Flower, abaxial. 2. Flower, adaxial. 3. Habit. 4. Achene & style. 5. Basal leaf. Drawn by A. DiNicola from *Ertter 21219* and corresponding live material, supplemented by field photos.

We are pleased with the opportunity to recognize Mark Darrach (b. 1957) by naming this new variety in his honor. He relocated the Greenhorn Mountains population, provided essential field support for the first author's visit to the site, subsequently located another population, and continued to assist in subsequent research on this new variety. Mark is a geologist-turned-botanist who has discovered and described several new species himself, mostly *Lomatium,* during his career with the Umatilla National Forest. He is also an avid Americana/Folk musician with a special fondness for Bernese Mountain Dogs. He runs a botanical and geological consulting business, Corydalis Consulting LLC. (pers. comm.; <oregonlive.com/pacific-northwest-news/index.ssf/2013/08/ore_botanist_ bushwhacks_in_rug.html>).

Figure 3. Plants of *Potentilla versicolor* var. *darrachii* at the type locality. The rock crevice habitat is not typical but provides better photographic contrast than bare ground. Photo by B. Ertter.

ACKNOWLEDGEMENTS

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NUEVA ESPECIE DE *SALVIA* (LAMIACEAE) DEL CENTRO DE MÉXICO

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RESUMEN

Se describe e ilustra como especie nueva para la ciencia a **Salvia guevarae** Bedolla & Zamudio, **sp. nov.**, proveniente de la porción sur de la Sierra Madre Oriental en los estados de Hidalgo, Querétaro y San Luis Potosí. Es una especie de corolas rojas marcadamente ventricosas, con labios cortos, ubicada en la sección *Holwayana*, dentro de esta sección es parecida a *S. involucrata*, de la que se diferencia por las brácteas y corolas rojas, cáliz con el labio superior cortamente acuminado, corola glabra en la base y pubescente en los dos tercios superiores, tubo con 5 papilas lingüiformes en su interior y labios de la corola desiguales. Adicionalmente se presenta una descripción ampliada de *S. involucrata*, donde se reconoce como sinónimo de ésta a *S. puberula* y se proporciona una clave para la determinación de las especies mexicanas de dicha sección.

ABSTRACT

Salvia guevarae Bedolla & Zamudio, **sp. nov.**, is described and illustrated as a species new to science. It occurs in the southern portion of the Sierra Madre Oriental in the states of Hidalgo, Querétaro, and San Luis Potosí. The new species has red, markedly ventricose corollas with short lips and belongs to sect. *Holwayana*. It is similar to S. *involucrata*, from which it can be distinguished by its red bracts and corollas, shortly acuminate upper calyx lip, corolla glabrous at the base and pubescent in the upper two-thirds, tube with 5 linguiform papillae inside, and unequal corolla lips. Additionally provided here are an extended description of *S. involucrata*, with *S. puberula* as its synonym, and a key for identification of the Mexican species of sect. *Holwayana*.

Durante la realización del proyecto Flora del Bajío y de Regiones Adyacentes se han descrito aproximadamente 137 especies pertenecientes a varias familias de plantas vasculares para los estados de Guanajuato, Querétaro y la parte noreste de Michoacán, lo que resalta la extraordinaria riqueza florística de la región (Bedolla y Zamudio, en prep.).

El caso de la familia Lamiaceae no es la excepción, pues durante la preparación del tratamiento de ésta, se han descrito 6 especies nuevas para la región: *Salvia calderoniae* Bedolla & Zamudio, *S. carrazae* Zamudio & Bedolla, *S. purepecha* Bedolla, Lara, & Zamudio, *S. xolocotzii* Bedolla & Zamudio, *S. zamoranensis* Zamudio & Bedolla, y *Stachys turneri* Rzed. & Calderón (Bedolla et al. 2011; Bedolla & Zamudio 2015; Rzedowski & Calderón 1995). En este trabajo se presenta una especie nueva de *Salvia* de corolas rojas marcadamente ventricosas, con labios cortos, proveniente de la porción sur de la Sierra Madre Oriental en los estados de Hidalgo, Querétaro y San Luis Potosí, en esta zona la planta ha sido colectada en múltiples ocasiones y existe bastante material que da cuenta de su variación y distribución.

En el herbario IEB varios especímenes de ésta permanecieron por más de 25 años erróneamente identificados como *Salvia involucrata* o *S. puberula* (especies morfológicamente

similares), hasta que al revisarlos con detalle se concluyó que se trata de una especie nueva para la ciencia, que en esta contribución se describe e ilustra como *Salvia guevarae*.

La especie nueva es semejante en su morfología a *S. involucrata* y *S. puberula*, éstas últimas son a la vez tan parecidas entre sí, que en este trabajo *S. puberula* es considerada un sinónimo de *S. involucrata*. En este artículo se ofrece primero una descripción ampliada de *S. involucrata*, para luego tratar a S. *guevarae* y contrastarlas.

Se revisaron ejemplares en los herbarios ENCB, FCME, IEB, QMEX, y MEXU para documentar la variación de la especie, esclarecer la distribución de los taxa implicados y elaborar los mapas correspondientes.

Resultados

Cavanilles describió en 1793 a *S. involucrata* como una especie de corola rosa marcadamente ventricosa, con la base de las hojas cuneadas y brácteas evidentes, rosas, que cubren el botón distal de la inflorescencia (caracteres observables en la ilustración que acompaña al protologo y en el lectotipo); mientras que Fernald (1900) distinguió a *S. puberula* por las hojas con la base ligeramente cordadas y brácteas caedizas (aunque éstas en realidad no fueron observadas), adicionalmente menciona otros caracteres distintivos, como: tallo cinereo puberulento, hojas deltado-ovadas, inflorescencia de 13 cm de largo, laxa con los verticilastros basales distanciados ca. de 2.5 cm, cáliz piloso-cetáceo, con los tricomas sobre las venas y el labio superior el doble de largo que el inferior; sin embargo, estos caracteres también están presentes en *S. involucrata*, por lo que en los herbarios se encuentran especímenes identificados indistintamente con alguno de estos nombres.

Epling (1939) reconoció a *Salvia involucrata* y *S. puberula* como especies válidas, aunque con cierta duda, él distinguió a *S. puberula* de *S. involucrata* por las hojas con la base cordada (*vs.* redondeada y estrecha, en ocasiones subcordada), distancia entre verticilastros de 2.5–4 cm (*vs.* 1–2 cm), cáliz de 15 mm de largo (*vs.* 12–13 mm) y corola de 28–30 mm de largo (*vs.* 21–33 mm). Al revisar los ejemplares tipo de ambas especies y el material depositado en los herbarios mexicanos se registró una amplia variación de estos caracteres; por ejemplo, la forma de la hoja varía de ovada, ovado-lanceolada a deltada; por otro lado, el grado de maduración influye en el largo de la inflorescencia, así como en la persistencia y tamaño de las brácteas. Ejemplares revisados de una misma colecta muestran plantas con brácteas en la parte distal de la inflorescencia o sin brácteas [*Rzedowski 44750* (ENCB, IEB); *Santillán 520* (ENCB, IEB); *Hinton et al.* 17485 (IEB, MEXU); *Hernández M. et al. 10946* (ENCB, IEB, MEXU)]; además también se observan diferencias en el tamaño de las brácteas, las que tienden a ser más pequeñas conforme se avanza hacia los verticilastros distales de la inflorescencia; sin embargo, la forma ovada a ovado lanceolada de las brácteas se mantiene al igual que el color rosáceo-purpúreo [*Hernández M. & Hernández 6542* (MEXU); *Guzmán 46* (IEB, MEXU); *González 218* (IEB, MEXU, QMEX)], por lo que se puede concluir que ambos nombres se refieren al mismo taxón.

Respecto a su distribución, no existe una distribución disyunta, por el contrario, la figura 1 muestra una franja continua que inicia en el S de Nuevo León y Tamaulipas y termina en el N de Puebla y centro de Veracruz. Algunos ejemplares provenientes de Chiapas estaban erróneamente identificados como *Salvia involucrata*; sin embargo, pertenecían a otras especies de la sección *Holwayana* Ramamoorthy (1984).

Esta especie es fácilmente distinguible por presentar pedúnculo y raquis con 2 tipos de tricomas glandulares, unos cortos capitados, casi sésiles, densamente distribuidos y otros de más de 1 mm de largo, esparcidos, cáliz rosáceo-purpúreo, puberulento, con tricomas largos glandulares y simples sobre las venas, y otros cortos capitados sobre toda la superficie, labio superior caudado de 4–8 mm de largo y corola rosáceo-purpurea, con el labio superior densamente viloso.

Aunque las descripciones originales de *Salvia involucrata* y *S. puberula* fueron detalladas para esa época (1700-1900), las mediciones se basaron en pocos ejemplares, incluso cuando Ramamoorthy (1983) designó el lectotipo para *S. involucrata* no incluyó una descripción, por ello, aquí se presenta una descripción extensa y detallada de *S. involucrata*, que incluye a *S. puberula* como sinónimo, incorporando toda la variación morfológica encontrada a lo largo de su distribución:

SALVIA INVOLUCRATA Cav., Icon. 2: 3, t.105. 1793. **LECTOTIPO**: cultivada en Madrid, España, a partir de semillas provenientes de México, *Anon s.n.* (MA 476225).

Salvia puberula Fernald, Proc. Amer. Acad. Arts. 35(25): 539–540. 1900. **TIPO: México**. San Luis Potosí. 1850–2460 m, 1878, *C.C. Parry & E. Palmer 755* (holotipo GH; isotipos BM, E, K, NY, PH, US).

Planta herbácea perenne, erecta, de hasta 2 m de altura. Tallo verde o teñido de morado, densamente puberulento a estriguloso, con tricomas simples multicelulares y en ocasiones con tricomas glandulares largos, estos últimos caedizos con la edad. Peciolo verde a morado, de 1–5(–9) cm de largo, disminuyendo notoriamente en longitud hacia arriba, hasta ser casi imperceptible en la base de la inflorescencia, pubescencia semejante al tallo. Hojas discoloras, haz verde obscuro, envés verde claro a grisáceo, lámina ovada, ovado-lanceolada a deltada, de (3–)6–14 cm de largo y 2–8 cm de ancho, ápice agudo, acuminado a caudado, base redondeada, ligeramente cuneada a truncada o cordada, margen crenado a serrado, haz esparcidamente piloso a glabrescente, envés puberulento a glabro, con tricomas esparcidos. Inflorescencia en racimos terminales laxos, de (5–)10–36(–50) cm de largo, con (3–)7–15(–34) verticilastros por inflorescencia, y 4–10 flores por verticilastro, pedúnculo y raquis con 2 tipos de tricomas glandulares, unos cortos capitados casi sésiles, densamente distribuidos y otros de más de 1 mm de largo esparcidos. Brácteas rosáceo-purpúreas, caedizas durante la dehiscencia, persistiendo temporalmente en la parte distal de la inflorescencia cubriendo al botón, ampliamente ovadas a ovado lanceoladas, de (3–)8–20 mm largo y (2–)7–14 mm de ancho, con el ápice ligeramente acuminado, el acumen recto, ligeramente curvo a uncinado, esparcidamente puberulentas a glabras, margen cortamente ciliolado, con venas reticuladas muy tenues. Cáliz rosáceo-purpúreo, campanulado, de 10–16 mm de largo y 3–7 mm de ancho, puberulento, con tricomas glandulares largos y tricomas simples sobre las venas, y otros cortos capitados sobre toda la superficie, tubo de 8–12 mm de largo, labios desiguales, el superior entero caudado, a veces con 2 pequeños dientes laterales mucronados, de 4–8 mm de largo, con 7 venas, el inferior con dos lóbulos caudados, de 2–4 mm de largo. Corola rosáceo-purpúrea, de 28–45 mm de largo, el labio superior densamente viloso, tubo de 25–36 de largo y 6–10 mm de ancho, marcadamente ventricoso, angostándose en una base cilíndrica de 6–7 mm de largo, invaginado, con 2 papilas lineares arqueadas de ±5 mm de largo, en el interior cerca de la base, con venas horizontales conspicuas a lo largo del tubo, labios subiguales, cortos, de 6–10 mm de largo, el superior galeado, el inferior trilobado, los lóbulos laterales reflexos, el medio oblato con el margen ligeramente ondulado, extendido, de 6–10 mm de largo y 4–6 mm de ancho,. Estambres cubiertos por la gálea, conectivos de 15–18 mm de largo, con un diente obtuso en la parte ventral, sin estaminodios. Estilo blanco de 35–40 mm de largo, escasa a densamente viloso, entre 5–7 mm, por debajo de la bifurcación, la rama superior más larga que la inferior. Mericarpos ovoides, triquetos, de 3–3.5 mm de largo y 1.7–2 mm de ancho, lustrosos, café obscuro variegado con manchas de color café claro.

Salvia involucrata se distribuye en la porción centro-sur de la Sierra Madre Oriental (subprovincias Gran Sierra Plegada, Sierras y Llanuras Occidentales y Carso Huasteco), en los estados de Nuevo León, Tamaulipas, San Luis Potosí, Guanajuato, Querétaro, Hidalgo, Puebla y Veracruz (Fig. 1). Crece en bosques de encino, pino y encino, mesófilo de montaña y en la vegetación secundaria derivada de éstos; ocupa un intervalo altitudinal de 1100 a 2600 m; florece y fructifica de julio a enero.
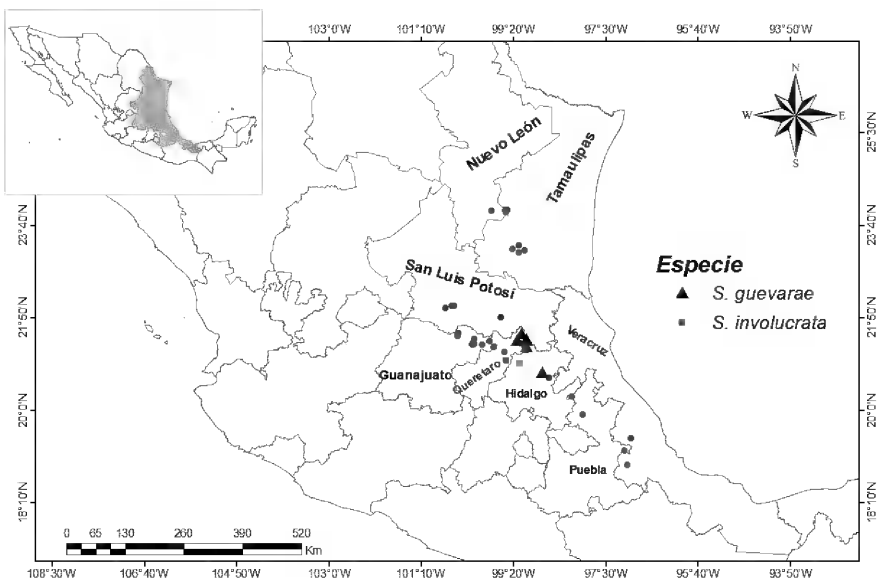
Figura 1. Distribución de *Salvia involucrata* y *S. guevarae*.

Material adicional revisado. México. Guanajuato. 2 km de Mesas de Jesús, por el camino al Vergel, municipio de San Luis de La Paz, 2300 m, 20 Jul 1992, *Díaz y García 7071* (IEB); alrededores de San Agustín, municipio de Victoria, 2400 m, 11 Sep 1987, *Rzedowski 44750* (ENCB, IEB); Puerto de Palmas, municipio de Victoria, 1970 m, 31 Oct 1987, *Santillán 520* (ENCB, IEB); Arroyo Blanco, cerca de Atarjea, municipio de Atarjea, 1300 m, 26 Nov 1987, *Santillán 626* (IEB); El Ocotero, 18 km al N de Xichú, municipio de Xichú, 2200 m, 04 Nov 1988, *Ventura y López 6300* (IEB); El Charco, 25 km al N de Xichú, municipio de Xichú, 2100 m, 11 Sep 1989, *Ventura y López 7285* (IEB, MEXU); El Puerto Blanco, 13 km al N de Mesas de Jesús, municipio de San Luis de La Paz, 2100 m, 06 Oct 1989, *Ventura y López 7435* (IEB, MEXU); Charco Azul, municipio de Xichú, 2200 m, 23 Ago 1990, *Ventura y López 8640* (IEB); cerro El Rosario, por Joya Fría, municipio de Victoria, 2200 m, 17 Oct 1991, *Ventura y López 9702* (IEB); Mesa de Jesús, municipio de San Luis de La Paz, 2100 m, 25 Oct 1991, *Zamudio y Pérez 8333* (IEB); ± 4 km al N de Mesas de Jesús por la brecha al Vergel, municipio de San Luis de La Paz, 1900 m, 19 Sep 2009, *Zamudio y Ramírez 14612* (IEB); ± 4 km al SW de El Toro, municipio de Atarjea, 2000 m, 21°22'32"N, 99°48'44"W, 21 Nov 2009, *Zamudio y Ramírez 14699* (IEB). **Hidalgo**. 4 km al E de Eloxochitlán, municipio de Eloxochitlán, 1925 m, 16 Ago 1995, *Alcántara 2267* (MEXU); 6.5 km al E de Eloxochitlán, municipio de Eloxochitlán, 1820 m, 14 Nov 1995, *Alcántara 2681* (MEXU); Molango a 5 Km del pueblo, enfrente del bosque, municipio de Molango de Escamilla, 13 Nov 1975, *Delgado S. y Hernández M. 74* (MEXU); 9.8 mi. al O de la carr. Pachuca-Tampico, Méx. 105, sobre el camino a Eloxochitlán, ca. 2 mi. al E de Eloxochitlán, municipio de Eloxochitlán, 2040 m, 06 Jul 1980, *Lott y Wendt P6* (MEXU); Rancho Viejo, municipio de La Misión, 28 jun 1964, *González-Quintero 1021* (IEB, MEXU); 45 km al E de Zacualtipan, municipio de Ixtlahuaco, 1600 m, 13 Ene 1980, *Hernández M. 4021* (MEXU); 2 km al W de Tianguistengo, municipio de Tianguistengo, 1700 m, 08 Nov 1980, *Hernández M. et al. 5373* (MEXU); Tepeoco, 5 km al NE de Zacualtipán, municipio de Zacualtipán de Ángeles, 2200 m, 14 Ago 1981, *Hernández M. et al. 6376* (MEXU); 30 km al NE de Zimapán, municipio de Zimapán, 1900 m, 13 Sep 1981, *Hernández M. e Hernández 6542* (MEXU); margen del Río Malila, 6 km al S de Molango, municipio de Molango de Escamilla, 1600 m, 15 Jul 1992, *López 221* (IEB, MEXU, QMEX);

ejido Zacualtipán, al SE de la población de Zacualtipán, municipio de Zacualtipán de Ángeles, 2020 m, 04 Ene 1993, *López G. 461* (MEXU); along Mexico Hwy. 85 between Tamazunchale and Zimapán, 54 km S of border with San Luis Potosí, 3 km N of Cuesta Colorada, at Rancho Viejo, 1600 m, 10 Oct 1985, *Spellenberg, Zucker y Zimmerman 8362* (MEXU) **Nuevo León**.   El Salto, municipio de General Zaragoza, 1460 m, 26 Oct 1978, *Hinton et al. 17485* (IEB, MEXU); cerro El Viejo, municipio de General Zaragoza, 1795 m, 16 Oct 1992, *Hinton et al. 22562* (IEB); cerro El Viejo, municipio de General Zaragoza, 1540 m, 20 Feb 1990, *Hinton et al. 22660* (IEB, MEXU, QMEX); cerro El Viejo, municipio de General Zaragoza, 1550 m, 01 Oct 1993, *Hinton et al. 23792* (IEB); Los Caballos, municipio de General Zaragoza, 1730 m, 02 Ago 1994, *Hinton et al. 24603* (MEXU).   **Puebla**.   ca. 6.7 km (vía road); W de Pahuatlán, municipio de Pahuatlán, [UTM zona_,588.9 km. E, 2242.1 km N. Nomenclator, 1987], 1450 m, 24 Jul 1988, *Bye & Linares 16435* (MEXU); Xopanapa, camino de Honey a Pahuatlán, 14 Sep 1945, *Miranda 3659* (MEXU); San Ignacio, 20 Jul 1910, *Nicolás s.n.* (MEXU); planta Trinidad, an abandoned hydroelectric plant. ca. 14.5 km NW of turnoff from Hwy. 130 at San Pedro Tlachichilco, 5 km beyond Honey, 1.5 km down from road, 1800 m, 23 Sep 1985, *Reisfield y Sunderberg 1213* (MEXU); cliff along trail between Honey and Pahuatlan, 1350 m, 14 Sep 1945, *Sharp 45915* (MEXU); al NE de Zacatlán, municipio de Zacatlán, 19 Nov 1987, *Tenorio, Villalobos C. y González V. 14210* (MEXU); 8 km al SW de Pahuatlán, municipio de Pahuatlán, 1800 m, 12 Ene 1987, *Toriz, Campos, Téllez y Tenorio 218* (MEXU). **Querétaro**.   N of Hwy 120 and El Madroño, near Valle de Guadalupe, municipio de Landa, 2145 m, 17 Nov 1971, *Boutin 3451* (MEXU); ± 2 km al WSW de Valle Verde, municipio de Jalpan, 1550 m, 01 Jul 1998, *Carranza y Zamudio 5530* (IEB); 0.5 km al SE de La Parada, municipio de Jalpan, 1100 m, 16 Dic 1987, *Chávez 206* (IEB); Puerto de las Navajas, ± 5 km al NE de Santa Inés, municipio de Landa, 1520 m, 06 Oct 1988, *González 218* (IEB, MEXU, QMEX); Puerto de la Joya Colorada, 5 km al W de La Florida, municipio de Landa, 1900 m, 17 Oct 1988, *González 245* (IEB, MEXU, QMEX); La Joya Colorada, 4 km al NE de la Florida, municipio de Landa, 1720 m, 05 May 1989, *González 595* (IEB); 1 km al N de La Parada, cerro Los Lirios, municipio de Jalpan, 1100 m, 31 Jul 1989, *Guzmán 37* (IEB); 1 km al N de El Naranjo, municipio de Landa, 1200 m, 31 Jul 1989, *Guzmán 46* (IEB, MEXU); 6 km al S de El Lobo, municipio de Landa, 1400 m, 31 Jul 1987, *Hernández M. 4077* (ENCB); brecha hacia San Juan Tetla, municipio de San Joaquín, 2200-2400 m, 25 Oct 1994, *Hernández M. et al., 10946* (ENCB, IEB, MEXU); 2 km al S de La Florida, por el camino a Xichú, municipio de Arroyo Seco, 1600 m, 21 Nov 1995, *Pérez y Zamudio 3249* (IEB); 2 km al S de La Florida, por el camino a Xichú, municipio de Arroyo Seco, 1600 m, 21 Nov 1995, *Pérez y Zamudio 3263* (IEB); El Banco, 2 km al NW de Puerto Hondo, municipio de Landa, 1830 m, 10 Sep 1988, *Rubio 130* (IEB, MEXU, QMEX); 1.5 km al E de Puerto Hondo, municipio de Landa, 1800 m, 12 Nov 1988, *Rubio 290* (IEB, QMEX); 1.5 km al SE de La Yesca, municipio de Landa, 1930 m, 15 May 1989, *Rubio 687* (IEB, MEXU, QMEX); 1 km al poniente del cerro El Colorín, municipio de Landa, 1420 m, 06 Sep 1989, *Rubio 1070* (IEB, MEXU); 1 km al E de La Mesa de Jagüey, municipio de Landa, 1350 m, 20 jun 1990, *Rubio 1733* (IEB, MEXU, QMEX); 1 km al SE de La Mesa del Jagüey, municipio de Landa, 1360 m, 26 Ago 1990, *Rubio 1886* (IEB, MEXU, QMEX); 1 km al poniente de El Aguacate, municipio de Landa, 1550 m, 14 Sep 1990, *Rubio 1966* (IEB, QMEX); Puerto de San Agustín, municipio de Landa, 1600 m, 05 Jul 1991, *Rubio 2454* (IEB, MEXU, QMEX); 1 km al SW de El Lobo, municipio de Landa, 1600 m, 01 Ago 1987, *Rzedowski 44039* (IEB); 10 km al NW de El Madroño, municipio de Landa, 1800 m, 01 Jul 1987, *Rzedowski 44114* (IEB); cerca de Tres Lagunas, municipio de Landa, 1700 m, 22 jun 1988, *Rzedowski 46720* (IEB); 1 km al S de El Pinalito, cerca de Madroño, municipio de Landa, 2000 m, 18 Sep 1997, *Rzedowski 53485* (IEB); 3-4 km al W de La Parada, municipio de Jalpan, 1450 m, 15 marzo 1990, *Servín 18* (IEB); 3-4 km al W de La Parada, municipio de Jalpan, 1350 m, 24 Abr 1990, *Servín 147* (IEB, QMEX); 8-10 km al S de San Juan de Los Durán, 1900 m, 24 Sep 1990, *Servín 537* (IEB, MEXU); 10 km al E de San Pedro Escanela, por la brecha a Jalpan, municipio de Pinal de Amoles, 1750 m, 03 Jul 1987, *Zamudio y Díaz 5294* (ENCB, IEB, MEXU); ladera N del cerro de San Nicolás, Molinitos, municipio de Peñamiller, 2300 m, 17 Nov 1987, *Zamudio 5983* (ENCB, IEB, MEXU, QMEX); cañada Las Avispas, 6-7 km al NE de San Juan de los Durán, 1950 m, 29 jun 1989, *Zamudio, Carranza y Fernández 7334 y 7354* (IEB); Joya del Cerro Prieto, entre La Lagunita de San Diego y El Llano Chiquito, municipio de Landa, 2190 m, 06 Feb 1997, *Zamudio 10180* (IEB); La Cercada, 1250 m, 21°29'32"N, 99°08'57"W, 13 jun 2002, *Zamudio y Steinmann 11979* (IEB); cañada Las Avispas, 1950 m, 21°27'9.2"N, 99°7'49.4"W, 25 Oct 2003, *Zamudio y Hernández 12637* (IEB).   **San Luis Potosí**.   near

microwave tower along Mexican Hwy 70 E of San Luís Potosí, municipio de San Luis Potosí, 2590 m, 25 Oct 1983, *Breedlove y Almeda 59298* (MEXU); alrededores del Llano del Conejo, al NE de Llano Chiquito, ± 10-12 km al NNW de Ahuacatlán, municipio de Xilitla, 2200 m, 13 Oct 1999, *Carranza y Zamudio 5923* (IEB); Sierra de Álvarez, 2100-2300 m, 30 Jul 1934, *Pennell 17815* (MEXU); Sierra Álvarez, in sierra E of San Luis Potosí, along the road to the microondas tower, about 28.8 mi E of the junction of Mexico Hwy 57 & 70 on the bypass N of San Luís Potosí, 2520 m, 02 Nov 1982, *Peterson, Strachan y Ahlenslager 846* (MEXU); alrededores de la Sierra de Álvarez, entrando por San Francisco, 2352 m, 12 Sep 2011, *Rodríguez C., Munguía y Castro-Castro 6365* (IEB); 3 km al SW de Calera, municipio de Zaragoza, 2400 m, 23 Sep 1955, *Rzedowski 6620* (MEXU); microondas La Tortuga, 10 km al W de Vicente Guerrero, municipio de Río Verde, 2660 m, 06 Jul 1985, *Tenorio, Ramamoorthy y Frame 9162* (MEXU). **Tamaulipas**. paraje Los Pocitos, 1.2 km en línea recta al SW de Julilo, municipio de Gómez Farías, 1640 m, 22 Oct 2009, *Carrillo y Piedra 5620* (IEB); 1 km al SE del Rancho El Julilo y 16 km al NE de Gómez Farías, municipio de Gómez Farías, 600 m, 21 Sep 1971, *González-Medrano, Olvera y Martínez 3631* (MEXU); camino a Ojo de Agua del Indio, 7 km al W de Rancho del Cielo, 1300 m, 07 Ago 1972, *González-Medrano, López-Franco y Dirzo 4295* (MEXU); 5 km al W del Rancho del Cielo, municipio de Gómez Farías, 1300 m, 07 Ago 1972, *González-Medrano, López-Franco y Dirzo 4337* (MEXU); 5 km al SE de Puerto Purificación, cerca de Galindo, camino a Conrado Castillo, municipio de Hidalgo, 1300 m, 12 Oct 1989, *González-Medrano, Juárez, Hernández y González 17242* (MEXU); 9 km al S de Revilla (Rancho Nuevo), 2450 m, 14 Oct 1989, *González-Medrano, Juárez, Hernández y González 17267* (MEXU); Sierra de Guatemala part of Sierra Madre Oriental between La Joya and Julilo, N of Rancho del Cielo, municipio de Gómez Farías, 1980 m, 19 Dic 1989, *Diggs, Hall y Crosthwaite 4188* (MEXU); Los Caballos, municipio de Hidalgo, 1675 m, 25 Ago 1994, *Hinton et al., 24675* (MEXU); Rancho Nuevo, municipio de Hidalgo, 2400 m, 10 Nov 1994, *Hinton et al., 25086* (MEXU). **Veracruz**. Sta. Ana Atzalan al N de Orizaba, 1300 m, 30 Dic 1967, *Rosas R. 901* (MEXU); La Orduña, municipio de Coatepec, 1300 m, 25 Feb 1975, *Zola 41* (MEXU).

SALVIA GUEVARAE Bedolla & Zamudio, **sp. nov.** TIPO: **MÉXICO. Querétaro**. Municipio de Landa, 6–7 km al NE de Lagunita de San Diego, bosque de pino-encino, abundante en ladera de cerro, alt. 2400 m, arbusto erecto de 1.50 m de alto, flor roja, nombre local "mirto de monte", 28 ago 1991, *H. Rubio 2573* (holotipo IEB; isotipos por distribuirse). Figura 2.

Salviae involucratae similis sed differt habitu fruticoso, bractea rubra ad apicem rotundata vel obtusa, calyce sparse puberulo trichomatibus simplicibus et glandulosis et labello superiore breviter acuminato, corolla rubra pubescenti sed basem versus glabra, intus tubi basis 5 papillas linguiformes ferenti, labello inferiore patenti.

Planta arbustiva de hasta 1.50 m de altura, algo ramificada. Tallo cuadrangular, acanalado, ramas pubescentes, glabrescente con la edad, con tricomas simples y capitados. Peciolo verde, delgado, acanalado, ligeramente arqueado, de (1.5–)3.5–7 cm de largo, puberulento, con tricomas simples y glandulares. Hojas discoloras, haz verde, envés verde pálido, lámina ovada a deltada, de 2.5–7(–12) cm de largo y (2.5–)4–7 cm de ancho, ápice agudo a obtuso, base ligeramente truncada, redondeada a cordada, margen irregularmente crenado-aserrado, haz rugoso, esparcidamente puberulento, con tricomas simples adpresos, más densos sobre la vena principal, envés puberulento, los tricomas distribuidos sobre las venas y con glándulas puntiformes traslúcidas o amarillas dispersas en la superficie. Inflorescencias en racimos terminales, laxos, de (5–)8–22 cm de largo, con 3–8 verticilastros, separados entre sí 1–4.5 mm, con 5–9 flores por verticilastro; pedúnculo y raquis pubescentes, con tricomas simples y glandulares. Brácteas deciduas durante la dehiscencia, persisitiendo temporalmente cubriendo el botón distal durante el desarrollo de la inflorescencia, rojas, obovadas a ampliamente ovadas, de 10–30 mm de largo y 8–16 mm de ancho, con el ápice redondeado a obtuso, con 6 venas principales que se ramifican formando una retícula, esparcidamente pilósulas, con tricomas traslucidos en la parte externa y el margen, glabra en la parte interna. Cáliz verde o teñido de rojo parcial o totalmente, campanulado a largamente campanulado, de 12–16 mm de largo y 8–12 mm de ancho, esparcidamente puberulento, con tricomas simples y glandulares

trasclúcidos, tubo de 8–11 mm de largo, labios iguales, de 4–6 mm de largo, el superior ovado a ampliamente ovado, cortamente acuminado, con 6–7 venas principales, el inferior dividido en dos lóbulos ovado-acuminados, con 7 venas principales. Corola roja, de 35–36 mm de largo, glabra en la base y pubescente en los dos tercios superiores, con tricomas simples multicelulares rojos, tubo de 25–29 mm de largo y 9–13 mm de ancho, marcadamente ventricoso, con 5 papilas lingüiformes diminutas en la base en el interior, labios desiguales, el superior galeado, de 7–9 mm de largo, el inferior más largo de 9–12 mm de largo y 8–12 mm de ancho, extendido, trilobado, el lóbulo medio ligeramente invaginado. Estambres insertos en la garganta, cubiertos por la gálea, filamentos de 3–4 mm de largo, conectivos de 16–18 mm de largo, con algunos tricomas sésiles y subsésiles en la porción ventral, anteras de 3–4 mm de largo, dos estaminodios claviformes de ± 2 mm de largo. Estilo blanco, de 39–45 mm de largo, barbado con tricomas teñidos de rojo, la rama superior (4–5 mm) más larga que la inferior (1–1.5 mm), esta última teñida de rojo. Mericarpos elipsoides, de 3–4 mm de largo y 2–2.5 mm de ancho, superficie brillosa pustulada, de color gris o café claro, variegada con manchas café obscuro.

Las poblaciones de esta especie se distribuyen en la porción sur de la Sierra Madre Oriental, en los estados de Hidalgo, Querétaro y San Luis Potosí (Fig. 1). Crece en cañadas y laderas de cerros formados por rocas calizas, en bosques de pino-encino y mesófilo de montaña. Altitud de 1800 a 2700 m. Florece y fructifica de (febrero) mayo a diciembre.

El epíteto especifico honra la memoria del botánico mexicano Fernando Guevara Fefer, quien fuera profesor de la Facultad de Biología de la Universidad Michoacana de San Nicolás de Hidalgo, estudioso del bosque tropical caducifolio, de la ecología de las malezas de México y especialista en el género *Bursera*, pero sobre todo un gran maestro y amigo.

Material adicional revisado. México. Hidalgo. 5 km al E de Eloxochitlán, municipio de Eloxochitlán , 2005 m, 98°46'12"N, 20°45'11"W, 26 Jun 1995, *Alcántara A. y Ortíz B. 2134* (FCME); 4 km al E de Eloxochitlán, municipio de Eloxochitlán, 1925 m, 98°46'31"N, 20°45'20"W, 16 Sep 1995, *Luna V. et al. 2543* (FCME). **Querétaro.** aprox. 5 km (en línea recta) al SE de San Juan de Los Durán, rumbo al cerro Grande, al E del manantial, municipio de Jalpan, 1890 m, 24 May 2012, *Carranza 7686* (IEB); El Chupadero, ladera SE del cerro Pinalito de la Cruz, municipio de Landa, 2330 m, 28 Dic 1989, *González 1365* (IEB); cerro Grande 6-7 km al NE de Lagunita de San Diego, municipio de Landa, 2500-2600 m, 27 Oct 1990, *Rubio 2052* (IEB); 5-6 km al NE de San Juan de los Durán, punto el Arroyo, municipio de Jalpan, 1500-1600 m, 21 Ago 1991, *Servín 1269* (IEB); cañada Las Avispas, 6-7 km al NE de San Juan de los Durán, municipio de Jalpan, 1950 m, 29 Jun 1989, *Zamudio et al. 7354* (IEB, MEXU); Joya del cerro Prieto entre la Lagunita de San Diego y el Llano Chiquito, municipio de Landa, 2190 m, 6 Feb 1997, *Zamudio y Pérez 10180* (IEB); ladera N del cerro Grande, ± 9 km al SE de San Juan de los Durán, municipio de Jalpan, 2600-2700 m, 21°25'59"N, 99°8'8"W, 22 Oct 2010, *Zamudio y Servín 14465, 15013* (IEB); ladera NW del cerro Grande, ± 8.5 km al SE de San Juan de los Durán, municipio de Jalpan, 2700 m, 21°26'00"N, 99°08'35.7"W, 23 Jun 2011, *Zamudio, Aguilar y Servín 15141* (IEB); ladera NW del cerro Grande, ± 8 km al SE de San Juan de los Durán, municipio de Jalpan, 1960 m, 13 Oct 2011, *Zamudio, Aguilar y Servín 15309* (IEB). **San Luis Potosí.** 2.2 km al NW de La Trinidad, por la vereda que va al Llano de la Garza, 2075 m, municipio de Xilitla, 21°25'18.9"W, 99°04'56.1"W, 26 Oct 2015, *Castillo-Gómez, Castillo y Reséndiz 1702* (IEB, QMEX); Llano del Conejo, municipio de Xilitla, 2200 m, 21°24.182' N, 99°5.087 W, 13 Oct 1999, *Zamudio y Carranza 11191* (IEB, MEXU, XAL); Llano del Conejo, municipio de Xilitla, 2200 m, 21°24'096"N, 99°5'087"W, 14 Jun 2000, *Zamudio, Ocampo y Reznicek 11425* (IEB); 2 km al NW de La Trinidad, por el camino al Llano de La Garza, municipio de Xilitla, *Zamudio, De Nova, Hernández, et al. 17167* (UAMIZ).
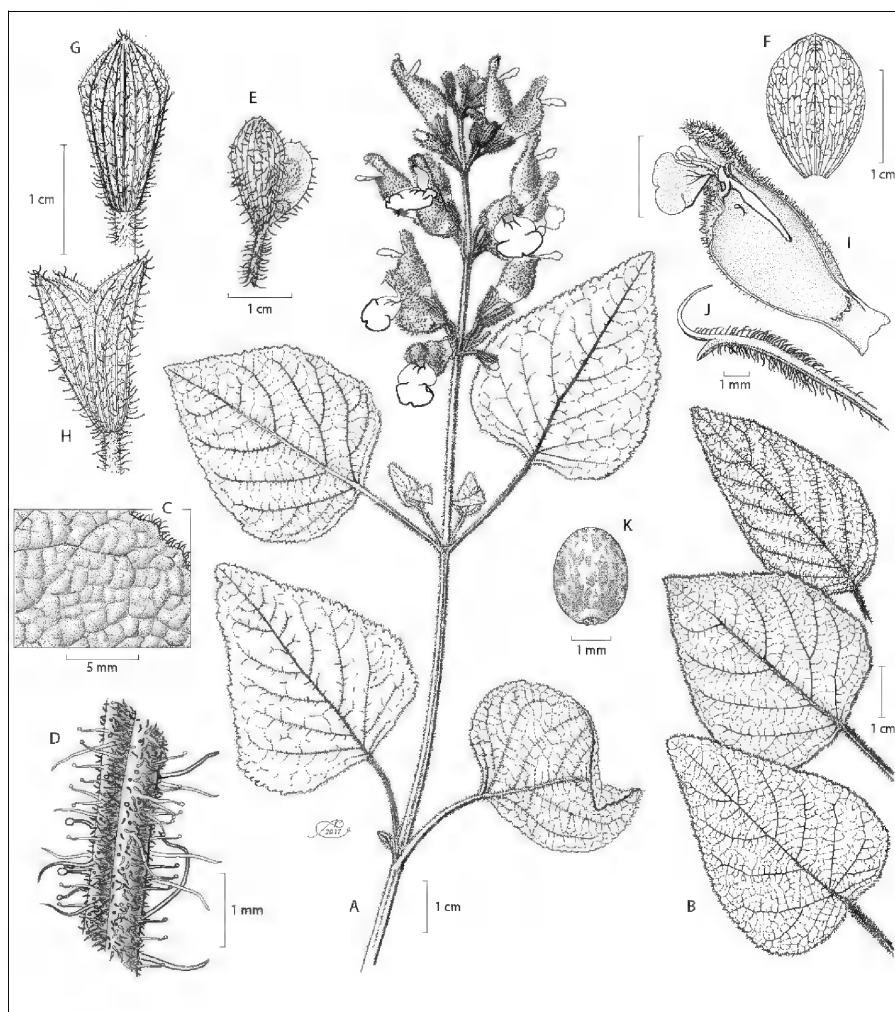
Figura 2. *Salvia guevarae*. A. Hábito. B. Diferentes formas de hojas. C. Detalle del haz de la hoja, se aprecia lo rugoso de la superficie y los cilios. D. Detalle de la pubescencia de la inflorescencia. E. Parte terminal de la inflorescencia mostrando las brácteas. F. Bráctea. G. Vista dorsal del cáliz. H. Vista lateral del cáliz. I. Vista lateral de la corola. J. Parte terminal del estilo. K. Mericarpo (basado en *H. Rubio 2573* (IEB), ilustrado por Alfonso Barbosa)

Salvia guevarae se ubica en la sección *Holwayana* Ramamoorthy (1984) por ser una planta arbustiva con hojas ovadas, base subcordada, verticilastros con muchas flores (5–9), brácteas tempranamente deciduas, de color rojo brillante y corola roja, con papilas en el interior del tubo.

Ramamoorthy (1984) conformó la sección *Holwayana* con 4 especies mexicanas (*Salvia holwayi* Blake, *S. karwinskii* Benth., *S. involucrata* Cav., *S. puberula* Fernald (considerara aquí

sinónimo de *S. involucrata*), *S. stolonifera* Benth., y *S. wagneriana* Polak) y 1 centroamericana (*S. siguatepequensis* Standl.). Estas especies inicialmente pertenecían a la sección *Cardinales* Epling (1939), pero cuando Ramamoorthy consideró a *S. cardinalis* como sinónimo de *S. fulgens*, (especie tipo de la sección *Fulgentes*), automáticamente el resto de las especies incluidas en la sección *Cardinalis* quedaron desprovistas de una sección, por lo que Ramamoorthy (1984) creó la sección *Holwayana*, para incluirlas. Adicionalmente, Santos (1991) durante la revisión de la sección *Nobiles* Epling, transfirió a las especies mexicanas *S. adenophora* Fernald, *S. disjuncta* Fernald, y *S. gesneriflora* Lindl. & Paxton a la sección *Holwayana*.

	Salvia guevarae	Salvia involucrata
HÁBITO	arbustiva	herbácea perenne
BRÁCTEA		
Color	roja	rosáceo purpúrea
Ápice	redondeado a obtuso	ligeramente acuminado, acumen recto, ligeramente curvo a uncinado
CÁLIZ		
Pubescencia	esparcidamente puberulento, con tricomas simples y glandulares	puberulento, con tricomas largos glandulares y simples sobre las venas, y otros cortos capitados sobre toda la superficie
Labio superior	cortamente acuminado	caudado
COROLA		
Color	roja	rosáceo purpúrea
Pubescencia	glabra en la base y pubescente en los dos tercios superiores	densamente vilosa sobre el labio superior
Invaginación	ausente	presente
Número de papilas	5	2
Forma de las papilas	lingüiformes	lineares y arqueadas
Proporción y largo de los labios	desiguales, superior 7–9 mm, inferior 9–12 mm	subiguales, ambos 6–10 mm
Posición de los lóbulos del labio inferior	Extendidos	extendidos, con el lóbulo medio oblato y los laterales reflexos

Cuadro 1. Comparación de caracteres entre *S. guevarae* y *S. involucrata*.

De las 9 especies que conforman actualmente la sección *Holwayana*, *Salvia guevarae* es parecida a *S. karwinski*, *S. wagneriana*, *S. involucrata*, y *S. holwayi* por los cálices con tricomas glandulares (algunas especies adicionalmente pueden presentar tricomas simples y dendríticos), tubo de la colora marcadamente ventricoso y labios cortos (5-10 mm de largo); sin embargo, *S. guevarae* se diferencia de este grupo por el tubo de la corola no invaginado, con 5 papilas lingüiformes diminutas en su interior, en contraste con el tubo de la corola invaginado con 2 papilas lineares arqueadas de las otras especies.

Salvia involucrata es la especie más parecida a *S. guevarae*, dado que ambas presentan hojas ovadas a deltadas, con la base redondeada, ligeramente truncada o cordada, inflorescencias de 8 a 36 cm de largo, con 4 a 10 verticilastros y 4 a 10 flores por verticilastro, corola de 30–45 mm de largo y tubo de 25–36 x 6–13 mm; sin embargo, las diferencias entre ambas especies radican esencialmente en que *S. guevarae* presenta brácteas y corolas rojas (vs. rosáceo-purpureas), cáliz con el labio superior cortamente acuminado (vs. caudado), corola glabra en la base y pubescente en los dos tercios superiores (vs. densamente vilosa sobre el labio superior), tubo con 5 papilas lingüiformes en su interior (vs. 2 papilas lineares y arqueadas), labios de la corola desiguales (vs. subiguales), otras diferencias se observan en el Cuadro 1 y en la Figura 3.

Figura 3. A. Hábito.   B. Porción de la inflorescencia. *Salvia involucrata*.   C. Hábito.   D. Porción de la inflorescencia (Fotografías de S. Zamudio).

A pesar de la simpatría de *Salvia involucrata* y *S. guevarae* en los estados de Querétaro (municipios de Jalpan y Landa) e Hidalgo (municipio de Eloxochitlán) y la similitud de su ubicación ecológica (bosques templados y mesófilo, altitud de 1100-2700 m), las dos especies no parecen tener

introgresión genética recíproca, las observaciones en campo y los ejemplares de herbario presentan los caracteres diagnósticos muy claros y definidos.

Es altamente probable que la sección *Holwayana* como está integrada ahora no forme una agrupación natural, por lo que en un futuro inmediato requerirá de una revisión taxonómica. Sin embargo, para fines prácticos se presenta una clave para identificar a las especies mexicanas de esta sección.

Clave para las especies mexicanas de *Salvia* sección *Holwayana*

1. Tubo de la corola sin papilas en el interior, cerca de la base.

  7. Flores solitarias, dispuestas en las axilas de las hojas .... **Salvia disjuncta**
  7. Flores agrupadas en inflorescencias racemosas terminales.

    8. Arbusto erecto; cáliz de 8–11 mm de largo; tubo de la corola de 18–22 mm de largo .... **Salvia adenophora**
    8. Arbusto escandente; cáliz de 11–25(–30) mm de largo; tubo de la corola de 30–40 mm de largo .... **Salvia gesneriiflora**

1. Tubo de la corola con papilas en el interior, cerca de la base.

  2. Tubo de la corola no invaginado cerca de la base, con 5 papilas lingüiformes diminutas en el interior .... **Salvia guevarae**
  2. Tubo de la corola invaginado cerca de la base, con 2 papilas longitudinales y arqueadas en el interior.

    3. Inflorescencia con el pedúnculo notablemente alargado (10–22 cm) sobresaliendo de las partes vegetativas; tubo de la corola infundibuliforme, labios de la corola mayores de 10 mm de largo .... **Salvia stolonifera**
    3. Inflorescencia con el pedúnculo corto (2.5–7 cm) sin sobresalir de forma evidente por encima de las partes vegetativas, tubo de la corola marcadamente ventricoso, labios de la corola menores de 10 mm de largo.

      4. Corola magenta, rosa a rosáceo-purpurea.

        5. Arbusto escandente; tallo café, glabro; hoja ovada a elíptica; cáliz piloso con densos tricomas glandulares largamente pedicelados sobre la superficie; labio superior del cáliz con el ápice mucronado, de 3–4 mm de largo .... **Salvia wagneriana**
        5. Herbácea perenne; tallo verde o teñido de morado, puberulento a estriguloso, con tricomas simples y en ocasiones con tricomas glandulares largos; hoja ovada, ovado lanceolada a deltada; cáliz puberulento con dos tipos de tricomas glandulares, unos largos sobre las venas y otros capitados sobre la superficie; labio superior del cáliz con el ápice caudado, de 4–8 mm de largo .... **Salvia involucrata**

      4. Corola roja.

        6. Indumento de tallos y hojas formado por tricomas dendríticos; cáliz de 12–17 mm de largo, labios subiguales de ± 8 mm de largo, el superior caudado; tubo de la corola de 18–25 mm de largo .... **Salvia karwinski**
        6. Indumento de tallos y hojas formado por tricomas simples; cáliz de 7–10 mm de largo, labios desiguales, el superior ovado a ligeramente caudado, de 4 mm de largo, el inferior de 2 mm de largo; tubo de la corola de 8–19 mm de largo .... **Salvia holwayi**

LITERATURA CITADA

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A NEW SPECIES OF QUARARIBEA (MALVACEAE) FROM COSTA RICA

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ABSTRACT

Some previous collections of *Quararibea nigrescens* have been misidentified, confused or tentatively assigned to *Quararibea costaricensis*. Both species, however, can be consistently distinguished because *Q. nigrescens* has always twigs, leaves and calyx conspicuously silvery or grayish lepidote or stellate-peltate pubescent, while in *Q. costaricensis* twigs and leaves are sparsely diminute tomentulose with dark brown fasciculate or rufous-brown stellate or stellate-peltate pubescent, becoming essentially glabrate with age, except, the calyx which possesses a dense pubescence of granuliferous-lepidote golden or greenish-brown trichomes. The proposed species name, *Q. nigrescens*, refers to the peculiar, unique and consistent dark gray, blackish to almost black color of leaves (mainly) that is noticeable upon drying, while in *Q. costaricensis* dried leaves are always conspicuously yellowish-green or yellowish-brown. This character (leaves color upon drying of *Q. nigrescens*) is unique among all Costa Rican species of *Quararibea*; additional morphological differences between both species are included.

RESUMEN

Algunas colecciones previas de *Quararibea nigrescens*, han sido mal identificadas, confundidas o tentativamente asignadas a *Quararibea costaricensis*. Ambas especies se distinguen consistentemente porque *Q. nigrescens* siempre tiene ramitas, hojas y flores (cáliz) con una pubescencia plateada o grisácea lepidota o estrellado-peltada conspicua, mientras en *Q. costaricensis* las ramitas y hojas tienen una pubescencia densa o esparcida diminuta con tricomas pardo-oscuro fasciculados o pardo-rojizo estrellado o estrellado-peltados, llegando a ser casi glabras con la edad, excepto, el cáliz que está cubierto densamente con tricomas dorados o pardo-verdoso granulado-lepidotos. El nombre propuesto, *Q. nigrescens*, obedece al color peculiar, único y consistente, gris oscuro, negruzco o casi negro de las hojas (principalmente) después del secado, mientras que en *Q. costaricensis* las hojas secas siempre se tornan conspicuamente verdoso-amarillentas o pardo-amarillentas después de secas. Este carácter (color de las hojas de *Q. nigrescens* después del secado) es único entre todas las especies de *Quararibea* de Costa Rica; otras diferencias morfológicas entre ambas especies se mencionan.

Quararibea Aubl. (Malvaceae, Bombacoideae) is a neotropical genus of mostly trees and treelets (rarely shrubs) from humid forests that comprises about 25 species, distributed from southern Mexico to South America. The genus is characterized by its, commonly, monopodial trunk and verticillate branching, simple and usually perennial leaves, axillary or cauliflorous flowers borne single, in fascicles or on short twigs, having an elongate staminal column, sometimes apically 5-lobed with numerous sessile anthers at the apex, and drupaceous indehiscent fruits (Alverson 1989; Gentry & Alverson 2001). The forthcoming treatment of the genus (A. Cascante, in prep.) for the Manual de Plantas de Costa Rica´s project recognizes 12 species of *Quararibea*, two of them are endemic to the country, including the one herein described as new.

QUARARIBEA NIGRESCENS N. Zamora, Cascante, & S.-Y. Kim, **sp. nov.** **TYPE: COSTA RICA. Alajuela**. Parque Nacional Rincón de la Vieja, puesto Santa María, del mirador siguiendo la fila hacia noreste, bajando al canal, 10º 46' N, 85º 18' W, 1100 m, 9 Mar. 1988 (fl.), *Herrera 1625* (holotype, CR; isotype, MO). Figures 1-2.

Differing from all other species of *Quararibea* known to us by its combination of conspicuously silvery or grayish lepidote or stellate-peltate pubescence and its unique consistent dark gray, blackish to almost black leaves color character upon drying. This new species has been previously misidentified or confused with *Quararibea costaricensis* Alverson, which it shares a similar floral morphology.

Tree of 5–15 m tall, 10–35 cm dbh; trunk monopodial or forked, cylindric, with smooth bark; plagiotropic branches usually horizontal and drooping, verticillate; young twigs slender, greenish-gray or grayish, sparsely to densely silvery, dark gray or blackish (when dry) lepidote or stellate-peltate pubescent towards the apex, older twigs reddish; **stipules** 4–9 x 1 mm, linear, densely lepidote pubescent, deciduous; stipule scars minute or not very conspicuous. **Leaves** simple, alternate, entire; petiole terete, 6–13 mm long, sparsely lepidote pubescent, lamina 6.3–19 x 3.5–7.5 cm, elliptic to ovate-elliptic, apex short acuminate to apiculate (acumen 1 cm), base oblique with one side rounded to nearly subcordate and the other obtuse to truncate, sparsely lepidote or stellate-peltate pubescent when young but soon glabrous above with the age, sparsely lepidote or stellate-peltate pubescent abaxially to almost glabrous with the age, only sparsely lepidote or stellate-peltate pubescent along main veins, sometimes conspicuously barbate (with domatia in the abaxial vein axils); secondary veins impressed above and prominent below, pinnate, 4–5 per side, weakly or pseudo trinerved at the base underneath (see, Fig. 1 and Fig. 2B, F), ascending, becoming brochidodromous near at the middle, tertiary veins reticulate on both sides and conspicuously dark gray or blackish to almost black upon drying. **Flowers** actinomorphic, usually solitary and opposite the leaves or sometimes borne on short lateral shoots, ramiflorous (up to 4 flowers), or from nodes, bending down to reflexed at anthesis (see, Fig. 2A, B); **pedicel** (8–)11–17 mm long, bearing usually 2–3 bracteoles, 1–2 mm long, subulate or scale like, at 4–7 mm apart from the base of the pedicel, more or less at middle length (rarely near the base), alternate, well-spaced or equidistant along length, lepidote pubescent; **calyx** narrowly conical, 6–8(–10) mm, blackish (when dry), densely silvery or dark grayish lepidote pubescent outside and dark brown hispid inside, lobes 3–5, 3 mm long; **petals** 5, white, asymmetrically and narrowly-oblanceolate to lanceolate, 13–17 x 3–4 mm, at the apex obtuse to acute, reflexed (in vivo), densely whitish-gray tomentulose pubescent on both sides, except glabrous towards the base; staminal column striate-cylindrical, 10–20 mm long, glabrous or sparsely stellate tomentulose; thecae many, reniform; style slightly exerted, stigma capitate. **Fruits** ovoid to ellipsoid, 3–5 x 1.7–2.8 cm, glabrous but densely gray-lepidote pubescent at the apex, finely longitudinally striate, yellow-green (fresh), blackish when dry, umbonate at the apex, bending down to reflexed at maturity (see, Fig. 2C, D); pedicels (10–)15–17 mm, bearing 2–3 persistent bracteoles; calyx cup of fruit persistent, accrescent, 8–10 mm long, covering ca. 1/3 of fruit length, irregularly lobed or erose at the apex. Seeds no seen.
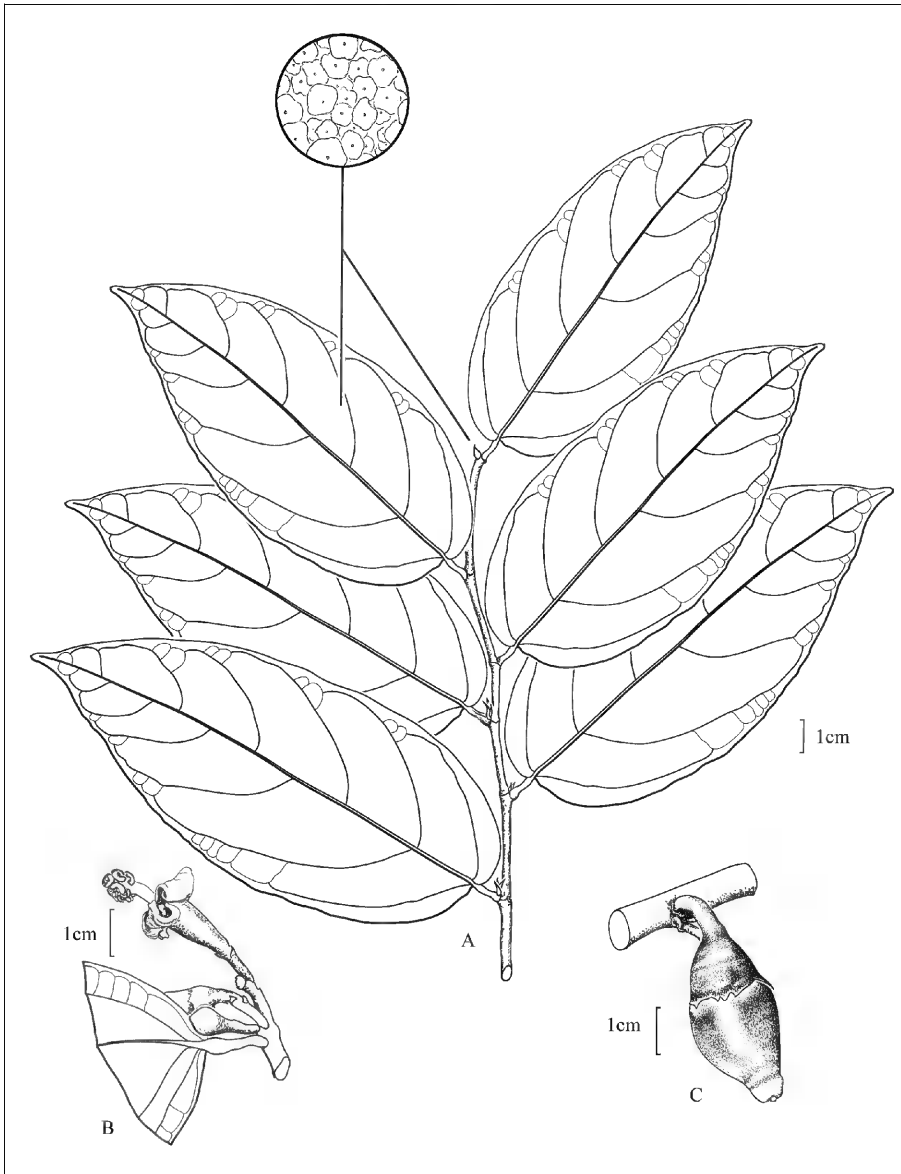
Figure 1. *Quararibea nigrescens*. A. Twig with leaves and lepidote pubescent detail (in circle) on the lamina and twig apex. B. Flower and flower buds. C. Fruit. Drawing by Claudia Aragón (All from *Zamora et al. 6158*).
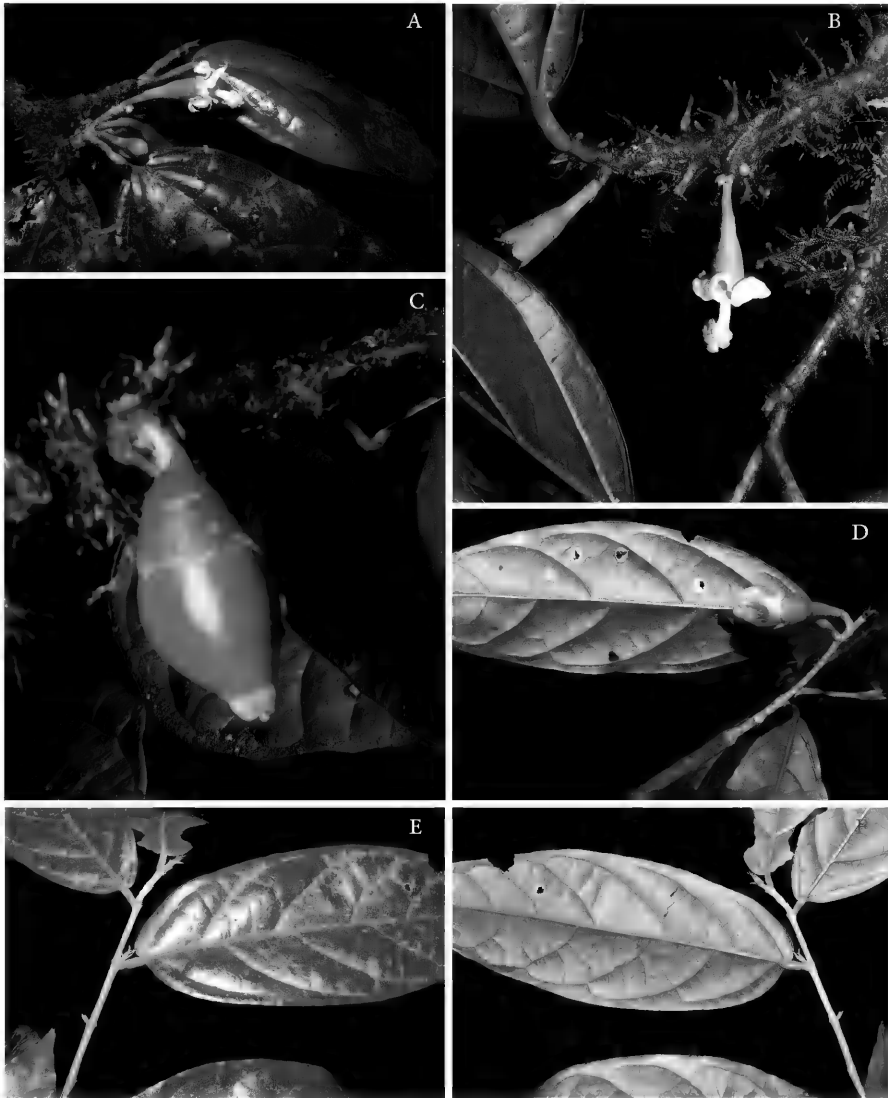
Figure 2. *Quararibea nigrescens*. A. Flower and flower buds. B. Flower with reflexed petals, bending down on old reddish twigs. C. Fruit shape, showing accrescent calyx cup. D. Fruit turning yellowish-green. E. Leaves upper surface and venation. F. Leaves underneath surface and venation. Photographs by N. Zamora. (All from *Zamora et al.* 6158).

Table 1. Differential characters between *Quararibea costaricensis* and *Q. nigrescens*. Measurements and characters for *Q. costaricensis* were taken from Alverson (1989).

| Character	Quararibea costaricensis	Quararibea nigrescens
Twigs and leaves pubescence	densely or sparsely diminute tomentulose with dark brown fasciculate or rufous-brown stellate or stellate-peltate	densely or sparsely diminute silvery, dark gray or blackish(when dry) lepidote or stellate-peltate
Stipules shape and scars	triangular, characteristically pale and conspicuous	mostly linear, dark and minute, not conspicuous
Leaf color upon drying	conspicuously yellowish-green or yellowish-brown	consistent dark gray, blackish to almost black
Pedicel length in flower	(4–)6–9(–11) mm	(8–)11–17 mm
Position of bracteoles on pedicels of flower	confined to lower part	equidistant and more or less at middle length
Calyx length in anthesis	9–13 mm	6–8(–10) mm
Calyx color, texture, and pubescence in flower	densely granuliferous-lepidote golden or greenish-brown	densely silvery lepidote, smooth and blackish
Calyx shape and length in fruit	urceolate to elongate-cupulate, accrescent covering ca. 1/2 of fruit, 15–25 mm	cup-shaped, accrescent covering ca. 1/3 of fruit, 8–10 mm
Petals shape and size (mm)	spathulate, 15–25 x 5–7	asymetrically and narrowly-oblanceolate to lanceolate, 13–17 x 3–4
Fruit color when dried	brown or reddish-brown	black

Habitat and distribution. *Quararibea nigrescens* is an endemic species to Costa Rica, so far only known from the Caribbean slope of Cordillera de Guanacaste, Cordillera de Tilarán and Cordillera Volcánica Central, at lower-middle elevation between 400–1100 m. It grows as an understory and subcanopy tree in wet and cloudy forest conditions classified as Humid and Wet Premontane Forest in the Holdridge Life Zones System (Bolaños & Watson 1993). The suggested related species *Q. costaricensis* occurs on both slopes (Pacific-Caribbean) and seems more commonly collected on the seasonal Pacific slope at middle and upland forests between elevations of (800-) 1100-1720 meters. *Quararibea costaricensis* is reported as intermittently deciduous (Alverson 1989), whereas *Q. nigrescens* is non-deciduous.

Phenology. Flowering specimens have been collected in March, May, June, and August; fruiting material in May and June.

Etymology. The specific epithet refers to the peculiar and consistent dark gray, blackish to almost black color of leaves upon drying.

Taxonomy and relationships. On morphological grounds, *Quararibea nigrescens* looks closely related to *Q. costaricensis* from which it has been previously confused in herbarium collections. Both species share a similar floral morphology, of more or less petals size and strongly reflexed at anthesis, but much longer pedicels, bracteoles positioned at the middle length and different petals shape in *Q. nigrescens*. The most notably qualitative character that separates both entities, is the blackish to almost black color of the leaf blade and fruit upon drying in *Q. nigrescens* versus yellowish-greenish to yellowish-brown in *Q. costaricensis*.

Moreover, frequently herbarium specimens of *Quararibea nigrescens* show leaves that appear much smaller, with fewer secondary veins numbers (sometimes barbate in the leaves axils) and twigs with inconspicuous stipule scars, compared to those of *Q. costaricensis*; additional differences are provided in Table 1. For more about *Q. costaricensis* relationships, see Alverson (1989).

Additional material examined. COSTA RICA. Guanacaste. Z. P. Tenorio, Tilarán, Cordillera Volcánica de Tilarán, Tierras Morenas, Finca El Sábalo, 10º 34' 50'' N, 84º 59' 30'' W, 685 m, 10 Ago 1993 (fl), *Rodríguez et al.* 181 (CR). **Alajuela.** Upala, Parque Nacional Tenorio, cuenca del río Zapote, Estación Heliconias, 10º 42' 45'' N, 85º 02' 27'' W, 700 m, 27 Abr 2001(fl buds), *Chaves et al.* 1160 (CR); San Ramón, Reserva Forestal de San Ramón, Sendero al SO del Río San Lorencito, 10º 13' 00'' N, 84º 37' 00'' W, 900-1100 m, 8 Abr 1993 (fr), *Gómez-Laur. et al.* 12405 (USJ); Cantón de San Carlos, Cordillera de Tilarán, 4 km SW of La Tigra, Río La Esperanza watershed, Araya-Ledezma farm, 10º 17' 00'' N, 84º 37' 00'' W, 500-600 m, 4 Mar 1993 (fr), *Haber et al.* 11438(CR, MO); Upala, Cuenca del Zapote, entrada La Camelia, saliendo de la Estación, 10º 43' 15'' N, 84º 59' 45'' W, 600-700 m, 19 May 2004 (fl), *Kriebel* 4597 (CR); Upala, Zapote de Upala, unos 2 kms antes del desvió al caserio Las Flores, 20 May 1975 (fl. bds), *Poveda s.n.* (CR, USJ); San Carlos, cuenca del Río San Carlos, San Carlos, La Fortuna, R. B. Arenal Mundo Aventura, 10º 27' 10'' N, 84º 39' 30'' W, 400 m, 27 May 2004 (fl), *Rodríguez* 8989 (CR); Guatuso, Área de Conservación Arenal-Tempisque, P. N. Tenorio, Estación El Pilón, 10º 42' 54'' N, 84º 59' 13'' W, 700 m, 20 Jun 2012 (fl, fr), *Zamora et al.* 6158 (CR, KIB); Upala, Dos Ríos, Buenos Aires, P. N. Rincón de la Vieja, sendero entrando por el albergue Sensoria, rumbo al cráter, parte media-baja del sendero, 10º 50' 58.3'' N, 85º 19' 38.2'' W, 1009 m, 28 Nov 2014 (str), *Zamora et al.* 7351(CR); Upala, Bijagua, Alto Los Brenes, Albergue Heliconias, Sendero circular. 10º 43' 22'' N, 85º 02' 12.5'' W, 700 m, 14 Jun 2016 (fl), *Zamora et al.* 8729 (CR); San Ramón. Reserva Biológica Manuel Alberto Brenes, cuenca media del Río San Lorencito, Estación Rodolfo Ortiz, Sendero al Volcán Muerto, 10º, 13' 07'' N, 84º 35' 54'' W, 900 m, 26 Ago 2017 (fl buds), *Zamora et al.* 9985 (CR).

ACKNOWLEDGEMENTS

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A SYNOPSIS OF *ASPIDOSPERMA* (APOCYNACEAE) IN MEXICO AND CENTRAL AMERICA WITH A TAXONOMIC CLARIFICATION OF *ASPIDOSPERMA CRUENTUM* AND A NEW CRYPTIC SPECIES

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ABSTRACT

We present a synopsis of *Aspidosperma* (Apocynaceae, Rauvolfioideae) in Mexico and Central America, recognizing seven species, including a new species described as **Aspidosperma crypticum** J.F. Morales & N. Zamora. *Aspidosperma cruentum* is accepted as a valid species and *A. desmanthum* and *A. spruceanum* are excluded of the Central America flora. A key to the species, relevant synonymy, and illustrations are included. Lectotypes are selected for *Aspidosperma excelsum* and *Geissospermum myristicifolium*.

Aspidosperma Mart. & Zucc. (Apocynaceae, Rauvolfioideae) occurs from southern Mexico to northern Argentina (excluding Chile) and the Antilles. The total number of accepted species has varied between monographs: Woodson (1951) recognized 52 species, whereas Marcondes-Ferreira (1988) accepted 34 and Potgieter (1999) 36 species. Floristics treatments or publications dealing with *Aspidosperma* also reported different species numbers during the last 26 years: 43 (Koch & Kinoshita 1999; Simões & Kinoshita 2002), 44 (Marcondes-Ferreira 1999; Morokawa et al. 2013; Pereira et al. (2016), 45 (Marcondes-Ferreira & Kinoshita 1996; Morales 2005), 46 (Morales 2009 a,b), 50 (Ezcurra 1981), and 55 Machate et al. (2016) among others. Therefore, the current number of species is uncertain. The intraspecific variation of some species makes *Aspidosperma* one of the most complex genera of the Neotropical Apocynaceae. Most species have a large number of synonyms and the circumscriptions of several species still need to be clarified.

Brazil is the center of diversity of *Aspidosperma* with more than 39 species reported, ten of them endemic there (Machate et al. 2016; Pereira et al. 2016). In contrast, Mexico and Central America have a low diversity, with only 6 species recorded (Potgieter 2010). However, some species have been involved in a dispute concerning the correct names that should be used for them.

Aspidosperma megalocarpon Müll. Arg. (1860), was the first species described for Mexico (Veracruz) and Central America. The type consists of a single collection with fruits. The fruit surface is smooth, without longitudinal ribs and with a short basal stipite.

Cufodontia Woodson (Woodson 1934a) was considered distinct from *Aspidosperma* by its bilobed calyx. Two species were described in the original publication: *C. lundelliana* Woodson and *C. stegomeris* Woodson. Woodson (1934b) described one additional species (*C. arborea* Woodson), increasing the number to three species. In the prologue, he stated that the fruits were unknown for the

three species. Matuda (1950) proposed *C. escuintlensis* Matuda, which was the first type collection with both flowers and fruits.

The type collection of *Aspidosperma lundellianum* Woodson from Campeche, Mexico, with flowers (bilobed calyx) and fruits, resembles *A. megalocarpon* (Woodson 1935). In the same publication, *A. cruentum* Woodson was described based on a fruiting collection from Guatemala. The type collection of *A. cruentum* has fruits with a conspicuous stipite ca. 3.5 cm long.

In the Flora of North America (Woodson 1938) reported three species of *Aspidosperma* in Mexico and Central America: *A. cruentum, A. lundellianum* Woodson, and *A. megalocarpon*. Lundell (1939) and Matuda 1950) described two additional species, *A. matudae* Lundell and *A. chiapense* Matuda, respectively, the last including a form (*A. chiapense* f. *tenax* Matuda).

Woodson (1951) reduced *Cufodontia* into *Aspidosperma*, proposing *A. stegomeris* (Woodson) Woodson and relegating the remaining species of *Cufodontia* and *A. lundellianum* into the synonymy (all with bilobed calyces). However, he relegated *A. cruentum, A. matudae, A. chiapense*, and *A. chiapense* f. *tenax* into the synonymy of *A. megalocarpon*, even though the differences on leaf venation, number of calyx lobes (5 vs 2), and fruit shape (conspicuously stipitate vs. shortly stipitate or non-stipitate). After this, *A. cruentum* would be involved in taxonomic confusion that would last more than 80 years.

Allen (1956), probably following Woodson (1951), included a detailed description and illustration of *Aspidosperma* (which matched with the type of *Aspidosperma cruentum*) but was named as *A. megalocarpon*. The voucher collection (*Allen 5544*, CR) has flowers with five sepals (instead of bilobed calyces as those reported in *A. megalocarpon*) and fruits with a well developed basal stipite (which is very small in *A. megalocarpon*).

Standley and Williams (1969) recognized two species of *Aspidosperma* in Guatemala, *A. megalocarpon* and *A. stegomeris*, probably following Woodson (1951). Nowicke (1970) reported *A. darienense* Woodson ex Dwyer and *A. megalocarpon* from Panama but followed Woodson (1951) and maintained *A. cruentum* in the synonymy.

Two unpublished monographs of *Aspidosperma* (Marcondes-Ferreira 1988; Potgieter 1999) have clarified the circumscription of *A. megalocarpon*, including in the synonymy *Cufodontia stegomeris, C. lundelliana, C. arborea, A. lundellianum,* and *C. escuintlensis*. They removed *A. cruentum, A. matudae,* and *A. chiapense* (including *A. chiapense* f. *tenax*) from the synonymy of *A. megalocarpon* and placed them under *A. spruceanum* Benth. ex Müll. Arg. or *A. desmanthum* Benth. ex Müll. Arg., respectively. Woodson (1951) reported *A. spruceanum* as endemic to northern Brazil, occurring on periodically inundated Amazonian forest, whereas *A. desmanthum* was distributed in Colombia, Venezuela, Guianas, and Brazil.

Morales (2005) accepted the circumscription proposed by Marcondes-Ferreira (1988), but in his treatment of the Apocynaceae of Guatemala and Honduras (Morales, 2009 a, b) he removed *Aspidosperma cruentum, A. matudae*, and *A. chiapense* from the synonymy of *A. spruceanum* (considered restricted to the Amazonian basin) and placed them under *A. desmanthum*, as proposed by Potgieter (1999). These works were overlooked by Pereira et al. (2016), who still reported *A. spruceanum* for Mexico and Central America.

Studying material for the Flora of Colombia series and working on a new treatment of the Apocynaceae of Panama, all the type collections of *Aspidosperma* reported for those countries have been examined. As result, we found that the name *A. desmanthum* has been misapplied for the

material of Mexico, Central America, and Colombia (partially), including collections of an undescribed species

In order to clarify the taxonomic confusion around *Aspidosperma cruentum* Woodson, (which need to be reinstated here as a valid species), we provide a brief synopsis of *Aspidosperma* in Mexico and Central America.

KEY TO THE SPECIES OF *ASPIDOSPERMA* IN MEXICO AND CENTRAL AMERICA

1. Calyx 2-lobed; follicles creamish-lepidote .... 5. **Aspidosperma megalocarpon**
1. Calyx 4-5-6-lobed; follicles tomentose, tomentulose, inconspicuously puberulent to glabrous or glabrate, black, ferrugineous, brown, white to creamish white.

  2. Trunk irregularly and longidutinally channelled; venation brochidodromous, secondary veins not parallel between them; follicles without longitudinal ribs.

    3. Corolla lobes 1.5–2 mm; fruits conspicuously and irregularly verrucose
    .... 4. **Aspidosperma excelsum**
    3. Corolla lobes 3–8 mm; fruits smooth.

      4. Twigs glabrous; calyx 5-lobed, sepals 1.5–2 mm; follicles glabrous, black when dry
      .... 7. **Aspidosperma rigidum**
      4. Twigs ferrugineous-tomentulose; calyx 2- or 4-lobed, sepals 2–4 mm; follicles tomentose or lepidote; tan, brown or ferrugineous when dry
      .... 6. **Aspidosperma myristicifolium**

  2. Trunk more or less cylindric or irregularly and longidutinally channelled (*A. darienense*); venation craspedodromous, secondary veins more or less parallel between them; follicles with or without longitudinal ribs.

    5. Calyx 5–6-lobed; inflorescence lateral and ramiflorous or axillary; follicles without longitudinal ribs .... 3. **Aspidosperma darienense**
    5. Calyx 5-lobed; inflorescence terminal or subterminal; follicles with longitudinal ribs.

      6. Trunk with milky sap, twigs with red o orange sap; leaf blades with 28–36 pairs of secondary veins; pedicels 1–3 mm; calyx lobes 1–2 mm long, glabrous on the inner surface; corolla lobes 1.3–2.2 mm; stipite 3.5–6 cm .... 1. **Aspidosperma cruentum**
      6. Trunk and twigs with milky sap; leaf blades with 38–50(+) pairs of secondary veins; pedicels 0–1.5 mm; calyx lobes 2.5–3.1 mm long, tomentulose only at the apex on the inner surface; corolla lobes 4–5 mm; stipite 1.5–3 cm .... 2. **Aspidosperma crypticum**

1. ASPIDOSPERMA CRUENTUM Woodson, Amer. J. Bot. 22: 634. 1935. **TYPE: GUATEMALA. Petén**. Uaxactún, 16 Apr 1931, *H. Bartlett 12750* (holotype: MO; isotypes: MICH, NY 00061273, S 04-1706, US 00111786). Figs. 1 A–D, 2A, 3B, 4.
Aspidosperma matudae Lundell, Phytologia 1: 339. 1939. **TYPE: MEXICO. Chiapas**. Escuintla, Jan 1938, *E. Matuda 2030* (holotype: MICH; isotypes: A 00057208, CAS 0000787, F 0095442F, 0095443F, photo F neg. 64654, GH 00057207, K 000975145, LL 00000191, LL 00372516, MEXU 00090166, MEXU 00537836, MO, NY, US 00111806).
Aspidosperma chiapense Matuda, Madroño 10: 172. 1950. **TYPE: MEXICO. Chiapas**. Escuintla, La Esperanza, 15 Feb 1946, *E. Matuda 16361* (holotype: MEXU [MEXU00109025]; isotypes: CAS, EAP 90583, ENCB, F 0092440F, photo F neg. 64015, MEXU 00090368, MICH, NY 00061274, US 00111784).

Aspidosperma chiapense Matuda f. *tenax* Matuda, Madroño 10: 173. 1950.   **TYPE: MEXICO. Chiapas**. Escuintla, La Esperanza, 25 Jan 1948, *E. Matuda 17386* (holotype: MEXU; isotypes: ENCB, F 0092439F, photo F neg. 63797, MEXU 00108898, MICH, NY 00061274).

Trees 8–40 m tall, trunk straight and cylindric, young branchlets somewhat angulate and densely adpressed-tomentulose, lepidote, subterete to terete when old, old branchlets with indument more sparse, drying olive green or tan, trunk with milky sap, twigs with red o orange sap. **Leaves**: blade 8–21 × 3.5–7.3 cm, narrowly elliptic to narrowly obovate-elliptic, the apex acute to shortly acuminate, the base obtuse to acute, glabrous on both surfaces (including the midvein), venation craspedodromous, with 28–36 pairs of secondary veins, tertiary veins more or less parallel to the secondary veins, petiole 18–31 mm. **Inflorescence** terminal, many-flowered, densely adpressed-tomentulose, peduncles 15–72 mm, pedicels 1–3 mm; calyx 5–lobed, lobes 1–2 × 0.8–1 mm, ovate, acute to obtuse at the apex, densely tomentulose externally, glabrous on the inner surface; **corolla** white to yellow, externally glabrous, tube 3.9–4.1 mm, lobes 1.3–2.2 × 0.3–0.4 mm, narrowly ovate, the apex acute, no twisted; anthers 0.6–0.7 mm, ovary ca. 1 mm, style-head ca. 0.4 mm. **Follicles** 21–24 × 9.5–12.5 cm, stipitate, the stipite 3.5–6 cm, obovoid, drying white to creamish white, densely tomentulose, usually with conspicuous longitudinal ribs, sometimes with a conspicuous medial rib, without lenticels; seeds 8–10 cm in diam.

Distribution. Mexico to Colombia.

Aspidosperma cruentum is easily distinguished by its corolla lobes not twisted, 1.3–2.2 mm length, calyx lobes 1–2 mm length, and fruits with a well developed basal stipite 3.5–6 cm length (fig. 2A). *Aspidosperma cruentum* is recognized again as a valid species after being included in the synonymy of *A. desmanthum*, *A. megalocarpon*, and *A. spruceanum* (e.g., Allen 1956; Woodson 1951; Marcondes-Ferreira 1988; Morales 2005, 2009 a,b). *Aspidosperma megalocarpon* differs by its bilobed calyx (a character uncommon in *Aspidosperma*), and lepidote fruits, without longitudinal ribs.

We agree with the circumscription of *Aspidosperma spruceanum* given by Woodson (1951) and (Potgieter 1999), partially with that of Pereira et al. (2016) (excluding the distribution range), and disagree with that of Marcondes-Ferreira (1988). *Aspidosperma spruceanum* should be considered restricted to the Amazonian basin. It is a remarkable species by its leaf blades, which are white abaxially (by the minute and dense glaucous indument). This character is easy to see even in dried specimens. In *A. cruentum* and *A. desmanthum*, sometimes the leaves are inconspicuously glaucous underneath when fresh, but turning to olive green or brown when dry.

Aspidosperma desmanthum should be also considered restricted to the Amazonian basin. The distribution range given by Potgieter (1999), Morales (2009 a,b), Potgieter (2010), and Pereira et al. (2016) is based on material of *A. cruentum*.

Lundell (1939) described the calyx lobes of *Aspidosperma matudae* ca. 2.6 mm length and corolla lobes ca. 3 mm, but the type has the calyx lobes ca. 2 mm length and corolla lobes ca. 2 mm length.

Representative specimens examined. MEXICO. Chiapas. Esperanza, Escuintla, 15 Aug 1948, *Maduta 18412* (JEPS, MEXU). **Quintana Roo**. La Unión, 9 km al N, 4 Mar 1980, *Téllez & Cabrera 1664* (MEXU, MO). **BELIZE. Cayo**. Hummingbird Highway, 19.5 mi S of Western Highway, 15 Jul 1995, *Atha & Walker 1156* (NY). **Orange Walk**. 3.6 km S of Program For Belize Camp, 12 May 1991, *Arvigo et al. 489* (NY, WAG). **Stann Creek**. Middlesey, 25 May 1939, *Gentle 2800* (K). **Toledo**. Firetail Creek, drainage into the Blades branch of the Monkey river, 4 Oct 2004, *Brewer 1859* (MO). **GUATEMALA. Petén**. Póptum, 21 Jan 1965, *Meneses 36* (USCG). **HONDURAS. Gracias a Dios**. Al N de Krausirpe, 7 Aug 1994, *House 2080* (TEFH).

NICARAGUA. Jinotega. San Andrés, municipio de Wiwili, reserva de Bosawas, comunidad de San Andrés, río Coco, 4 Feb 2006, *Coronado et al. 3335* (MO). **Rio San Juan**. Municipio El Castillo, refugio Bartola, 15 Feb 2005, *Rueda et al. 17872* (MO). **COSTA RICA. Cartago**. Cajón de Turrialba, 15 May 1974, *Poveda s.n.* (CR). **Heredia**. Sarapiqui, llanura de San Carlos, Los Arbolitos, al N de Puerto Viejo, 4 km aguas arriba unión Río Toro y Sarapiquí, 9 Mar 1993, *Araya 198* (CR, MO). **Puntarenas**. Esquinas, area between Rio Esquinas and Palmar Sur de Osa, 22 May 1950, *Allen 5544* (CR, MO). **San José**. Tarrazú, zona protectora Cerro Nara, entre Cruce de Quebrada Llano Grande y camino al acueducto, 8 Mar 2008, *Morales 16238* (CR). **PANAMA. Coclé**. Road to Coclesito W fork of Rio Rancheria, 8 Dec 1983, *Churchill et al. 3972* (MO, WAG). **Colón**. Santa Rita ridge, E of transisthmian highway, 16 Dec 1972, *Gentry 6560* (CR, MO). **Panama**. Barro Colorado Island, Canal Zone, 6 Mar 1969, *Croat 8421a* (CR, MO). **San Blas**. Cerro San José, continental divide between Cangandi and San Jose, 5 Feb 1986, *de Nevers & Herrera 7015* (MO).
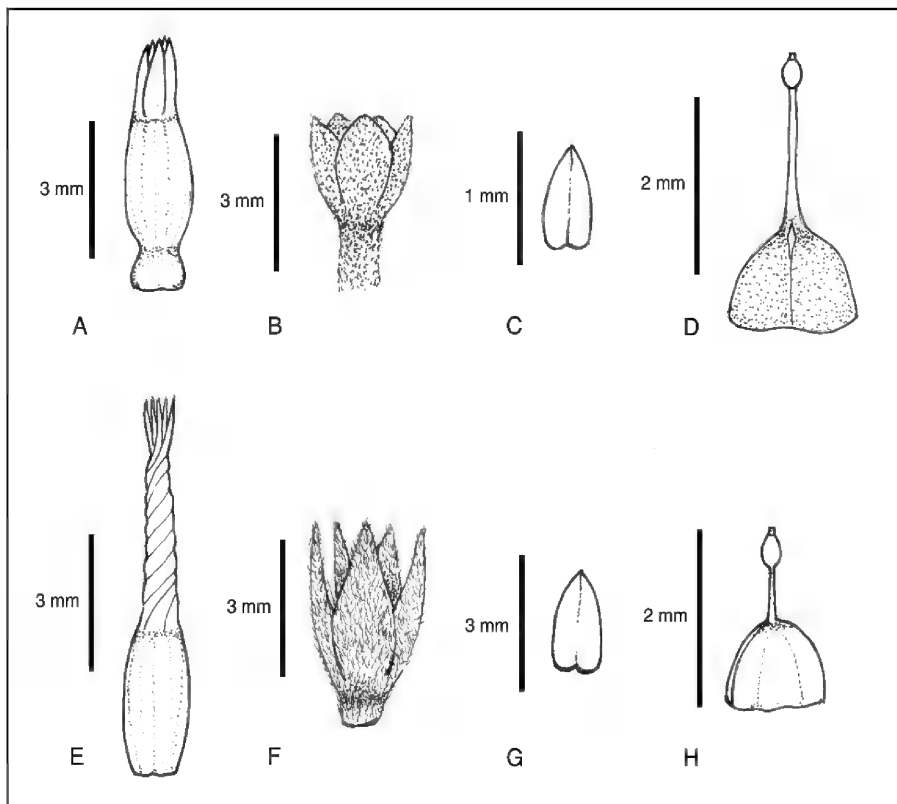

Figure 1. Flowers in *Aspidosperma*. *A. cruentum* (A-D *Thomsen 859*, CR). *A. crypticum* (E-H, *Aguilar et al. 871*, USJ). A, E. Corolla. B, F. Calyx. C, G. Anther. D, H. Ovary, style, and style-head.

2. ASPIDOSPERMA CRYPTICUM J.F. Morales & N. Zamora, **sp. nov.** TYPE: COSTA RICA.
Puntarenas. Refugio de Vida Silvestre Golfito, 3 km al N del aeropuerto, 26 Jan 1992,
Aguilar, Martín, Formoso, & Grayum 871 (holotype: CR; isotypes: MO, USJ). Figs. 1 E–H,
2B, 5.

Aspidosperma crypticum J.F. Morales & N. Zamora resembles *A. desmanthum* Benth. ex Müll.
Arg, but differs by its white latex (vs. red), leaf blades acute to shortly acuminate at the apex (vs. rounded
to obtuse or acute), with 38–50(+) pairs of secondary veins (vs. 21–26), corolla yellow (vs. white), and
larger follicles (13–15 × 10–11 cm vs. 10.4-10.6 × 6.8-7.2 cm). It is also similar to *A. cruentum* Woodson,
but *A. crypticum* has linear corolla lobes (vs. narrowly ovate) and fruits with the stipite 1.5–2 cm (vs. 3.5–
6 cm).

Trees 8–40 m tall, trunk straight and cylindric, young branchlets subterete to terete and
densely lepidote puberulent, old branchlets sparsely puberulent to glabrescent, drying black, trunk and
stems with conspicuous milky sap. Leaves: blade 10.5–21 × 3–6.3 cm, narrowly elliptic, the apex
acute to shortly acuminate, the base obtuse to acute, glabrous on both surfaces (including the
midvein), venation craspedodromous, with 38–50(+) pairs of secondary veins, tertiary veins more or
less parallel to the secondary veins, petiole 19–33 mm. Inflorescence terminal, many-flowered,
densely papillate-puberulent, peduncles 15–68 mm, pedicels 0–1.5 mm; calyx 5-lobed, lobes 2.5–3.1
× 0.8–1.1 mm, ovate, acute at the apex, densely tomentulose externally, tomentulose only at the apex
internally; corolla white, externally glabrous, tube 3.9–4.1 mm, lobes 4–5 × 0.2–0.3 mm, linear, the
apex long acuminate, twisted; anthers 0.7–0.8 mm, ovary ca. 1 mm, style head ca. 0.4 mm. Follicles
13–15 × 10–11 cm, stipitate, the stipite 1.5–2 cm, obovoid, dark brown when old, densely
tomentulose, usually with conspicuous longitudinal ribs, sometimes with a conspicuous medial rib,
without lenticels; seeds 7–8.5 cm in diam.

Distribution. Costa Rica, Panama, and Colombia, in tropical wet forest, at 0–700 m.

Aspidosperma crypticum has been misidentified as *A. desmanthum* Benth. ex Müll. Arg.,
which is otherwise restricted to the Amazonian basin. It differs from *A. desmanthum* by its white
latex (vs. red), leaf blades with 38–50(+) pairs of secondary veins (vs. 21–26), acute to shortly
acuminate at the apex (vs. rounded to obtuse or acute), corolla yellow (vs. white), and larger follicles
(13–15 × 10–11 cm vs. 10.4-10.6 × 6.8-7.2 cm). Sterile or flowering material resembles *A. cruentum*,
but *A. crypticum* is separated by the characters summarized in the key.

Specimens examined. COSTA RICA. Puntarenas. Golfito, entre el Pueblo de Bahia Chal
y Punta Camibar, 14 Dec 1991, *Aguilar 743* (CR, MO); Refugio de Vida Silvestre Golfito, 3 km al N
del aeropuerto, 29 May 1993, *Morales et al. 1530* (CR, MO). San José. Puriscal, cuenca del Tulín,
Fila Cangreja, costado Sur, 15 Sep 1998, *Acosta 25* (CR, MO); Tarrazú, cerros Diamante, camino a
Quepos, 28 Jan 1998, *Estrada 1442* (CR, MEXU); Zona Protectora La Cangreja, Santa Rosa de
Puriscal, Rio Negro, 12 Aug 1992, *Morales 358* (CR, MO). PANAMA. Panama. Along Llano-Cartí
road, near Nussagandi, 21 Jul 1986, *McPherson 9752* (CR, MO). COLOMBIA. El Valle.
Buenaventura, Cartón de Colombia timber concession, near Bajo Calima, 11 Feb 1984, *Juncosa 2121*
(CR, MO).

3. ASPIDOSPERMA DARIENENSE Woodson ex Dwyer, Ann. Missouri Bot. Gard. 53: 104. 1966.
TYPE: PANAMA. Darién. Between Chucunaque river and Canglón river, 12 Jun 1961,
Sexton & Knight s.n. (holotype: MO 2958523). Figs. 2C, 5.
Aspidosperma helstonei Donsel., Acta Bot. Neerl. 21(3); 253. 1972. TYPE: SURINAME. District
Brokopondo, E bank of Suriname river, SW of Redi Doti, 27 Jul 1964, *Donselaar 1487*
(holotype: U 0000474; isotypes: K 000587702, NY 00297970).

Distribution. Panama, Colombia to Brazil and Ecuador.

Aspidosperma darienense is distinguished by its leaf blades with more than 45 pairs of secondary veins, lateral inflorescences, 5-6-lobed calyx, and minutely lenticellate fruits, without longitudinal ribs.

Representative specimens examined.   PANAMA. Darién. Entre río Chucunaque y Chiatí, cerca del poblado de Buena Vista, 1 Apr 2001, *Quiroz s.n.* (PMA). **San Blás**. Montañas encima de Puerto Obaldia, 18 Aug 1971, *Gentry 1497* (MO).
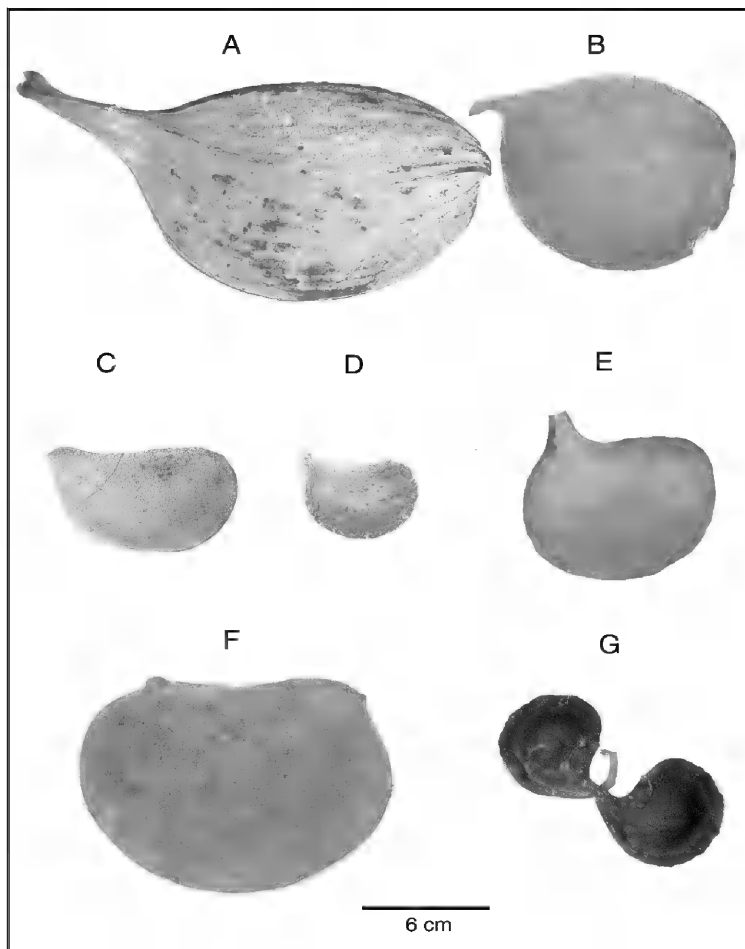

Figure 2. Fruits in *Aspidosperma*. A. *A. cruentum* (*Zamora et al. 1487*, CR). B. *A. crypticum* (*Morales 358*, CR). C. *A. darienense* (*Dik 438*, MO). D. *A. excelsum* (*Morales s.n.*, CR). E. *A. megalocarpon* (*Morales s.n.*, CR). F. *A. myristicifolium* (*Morales et al. 18648*, CR). G. *A. rigidum* (*Zamora et al. 2088*, CR).
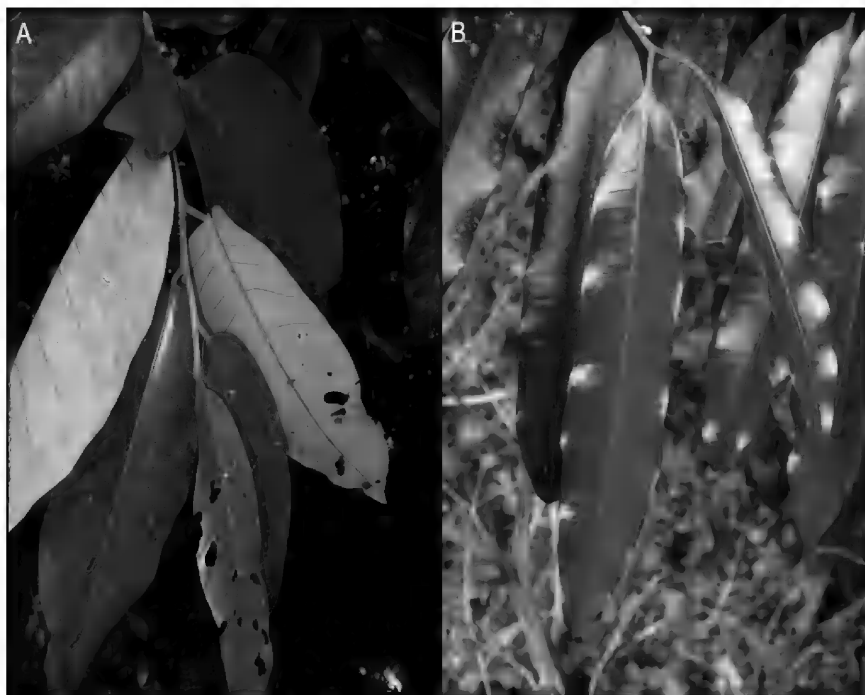
Figure 3.   Venation types in *Aspidosperma*.   A. Brochidodromous (*A. myristicifolium,* Morales 21437, USJ). B. Craspedodromous (*A. cruentum,* Morales 6601, CR).

4. ASPIDOSPERMA EXCELSUM Benth., J. Bot. (Hooker) 3: 245. 1841. *Macaglia excelsa* (Benth.) Kuntze, Revis. Gen. Pl. 2: 416. 1891. LECTOTYPE (here designated): **GUYANA**. Berbice, 1837, *Schomburgk 468* (K 000975141; isolectotypes, B [destroyed, photo F neg. 4409], BR 0000006956097, G 00169287, G 00169288, K 000587685, L 0931170, MO 2598572, P 00645106, RB, TCD 0006575, W). Figs. 2D, 5.

Distribution. Costa Rica to Brazil and Bolivia.

Woodson (1951, p. 171) designated *Schomburgk 468* as the type of *Aspidosperma excelsum* but without indicating a specific herbarium. Following the article 9.15 of the Code, we have selected a specific specimen as the lectotype.

In Mexico and Central America, three species have deeply and irregularly channelled trunk: *Aspidosperma excelsum, A. myristicifolium,* and *A. rigidum. Aspidosperma excelsum* is differentiated by its corolla lobes 1.5–2 mm and verrucose follicles.

Representative specimens examined. COSTA RICA. Limón. Talamanca, Amubri, 24 Jun 1989, *Hammel et al. 17510* (CR, F, MO). PANAMA. Colón. Santa Rita lumber road, 15 km E of Colón, 21 Mar 1968, *Dressler 3440* (F, GH, MO). Panamá. Alto de Pacora, 21 Mar 1997, *Galdames 3765* (MO, PMA). San Blas. El Llano-Cartí road, km 26.5, 11 Apr 1985, *de Nevers et al. 5827* (MO).
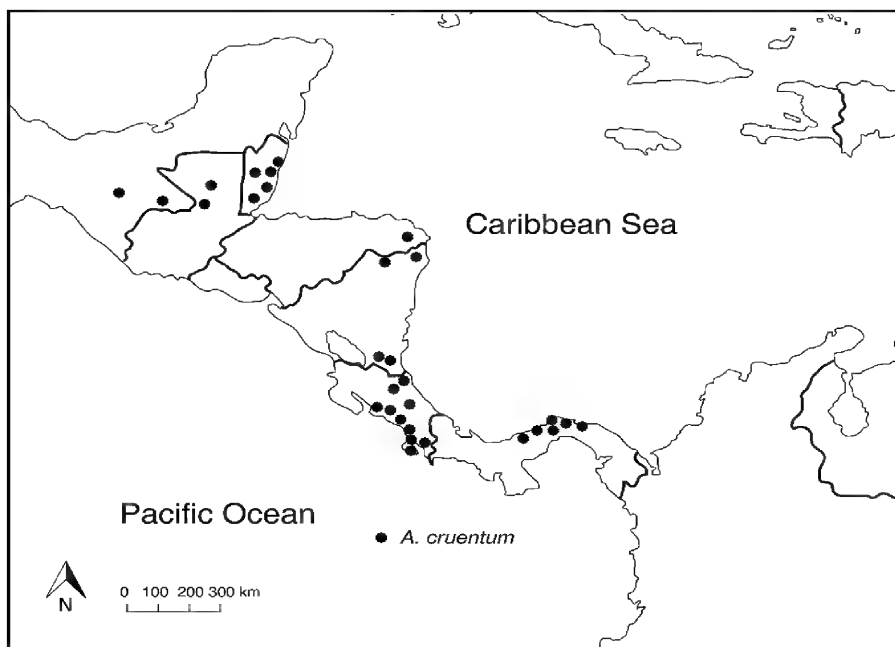
Figure 4. Distribution of *Aspidosperma cruentum*.

5. ASPIDOSPERMA MEGALOCARPON Müll. Arg., Linnaea 30: 400. 1860. *Macaglia megalocarpa* (Müll. Arg.) Kuntze, Revis. Gen. Pl. 2: 416. 1891. **TYPE: MEXICO. Veracruz**. Colipa, 1841-1842, *Karwinsky 1348* (holotype: LE). Figs. 2E, 6

Cufodontia stegomeris Woodson, Arch. Bot. Sist. 10: 39, t. 2. 1934. *Aspidosperma stegomeris* (Woodson) Woodson, Ann. Missouri Bot. Gard. 38: 178, f. 10. 1951. **TYPE: COSTA RICA. Puntarenas**. Finca Santa María, Jiménez, 31 Mar 1930, *Cufodontis 220* (holotype W [photo F neg. 30935]; isotypes: F 0048156F, photo F neg. 56460, G 00169400; MO 2958639).

Cufodontia lundelliana Woodson, Arch. Bot. Sist. 10: 40. 1934. **TYPE: GUATEMALA. Petén**. La Libertad, 26 May 1933, *Lundell 3408* (holotype: MO; isotypes: F 0048155F, photo F neg. 56459, GH 00078694, K 000587636, LL 00000192, MICH, NY 00298027, S 04-1872, US 00111772).

Aspidosperma lundellianum Woodson, Amer. J. Bot. 22: 684. 1935. **TYPE: MEXICO. Campeche**. Tuxpeña, 4 Feb 1932, *Lundell 1284* (holotype: MO 2958640; isotypes: F, 0092441F, photo F neg. 56433, GH 00057212, NY, US 00111804).

Cufodontia arborea Woodson, Ann. Missouri Bot. Gard. 21: 617. 1934. **TYPE: MEXICO. Oaxaca**. Cafetal, Concordia, 1-15 Apr 1933, *Morton & Makrinius 2692* (holotype: US; isotypes: CAS 0001589, F 0048153F, photo F neg. 56458, K 000587635, MICH 1111545, US 00111771).

Cufodontia escuintlensis Matuda, Madroño 10: 174. 1950. **TYPE: MEXICO. Chiapas**. Calcuta, Acacovagua, 17 Aug 1947, *E. Matuda 16978* (holotype: MEXU 00025418; isotypes: CAS 0001590, CAS 0001591, EAP 90592, F photo F neg 51100, MEXU 00025419, NY 00298026, US 01013868)

Distribution. Mexico to Colombia.

Aspidosperma megalocarpon is easily differentiated by its bilobed calyx, corolla lobes 5–6 mm and fruits without longitudinal ribs.

Representative specimens examined. MEXICO. Campeche. Champotón, 20 km E de Carlos Salinas de Goltari, camino a El Pozo, 19 May 1998, *Martínez et al. 30880* (M, MEXU). **Chiapas**: Ocosingo, comunidad Lacandona de Lacanha-Chansayab, 130 km SE de Palenque, 15 Feb 1994, *Levy & Durán140* (MEXU). **Oaxaca**. Tehuantepec, Santiago Astata, Panauhithu, El Aguaje, 1 Apr 2009, *Lott et al. 5845* (MEXU). **Veracruz**. Along road to Hotel Las Cabañas, Playa Escondida, Las Tuxtlas región, 31 May 1981, *Gentry et al. 32502* (CR, MEXU, MO). **GUATEMALA. Escuintla**. Nueva Concepción, finca Santa Marta, s.d., *Ruano s.n.* (BIGU). **Petén**. Lago Petén Itzá, ca. 1.3 km NNE-NE of San José, 28 Aug 1993, *Wallnöfer et al. 6073* (M, U, USCG, W). **Retalhuleu**. around Retalhuleu, 17 Feb-1 Mar 1941, *Standley 80803* (F, MO). **BELIZE. Cayo**. Valentín, Jun-Jul 1936, *Lundell 6220* (MO, NY). **Toledo**. Las Sierritas, 20 km W of Big Creek, 7 Dec 1997, *Hawkins 1731* (CR, MO). **HONDURAS. Comayagua**. Río Sulaco, al N de Santa Cruz de Yojoa, 18 Feb 1981, *Nelson et al. 7648* (MO, TEFH). **EL SALVADOR. Ahuachapán**. San Francisco Menéndez, San Benito, 20 Feb 1992, *Sandoval & Chinchilla 272* (B, LAGU, MO). **Cabañas**. Cinquera, quebrada la Creciente, 22 Apr 2001, *Carballo et al. 301* (CR, LAGU, MO). **NICARAGUA. Estelí**. 24 km al N de Estelí, 19 Dec 1984, *Moreno 25159* (MO). **COSTA RICA. Guanacaste**. Parque nacional Barra Honda, Los Mesones, 25 Sep 1991, *Zamora et al. 1869* (CR, MO, USJ). **Puntarenas**. Golfito, Dos Brazos de Río Tigre, Jiménez, 1 Sep 1990, *Herrera 4190* (CR, MO). **San José**. Reserva biológica Carara, sector Agrominas, 20 Sep 1991, *Zuñiga 460* (CR, MO). **PANAMA. Chiriquí**. Burica Peninsula, along quebrada Punta de Piedra, 2 mi SW of Puerto Armuelles, 1 Mar 1973, *Croat 22450* (CR, MO, USF, WAG). **Darién**. Cerro Tacarcuna, along río Pucuro, above Pucuro, 8 Feb 1975, *Gentry & Mori 14189* (MO).

6. ASPIDOSPERMA MYRISTICIFOLIUM (Markgr.) Woodson, Ann. Missouri Bot. Gard. 38: 169. 1951. *Geissospermum myristicifolium* Markgr., Notizbl. Bot. Gart. Berlin-Dahlem 11(108): 787. 1933. **LECTOTYPE** (here designated): **ECUADOR. Guayaquil**. Guayas, 1799, *Tafalla s.n.* (MA 814484; isolectotypes, B [destroyed], G, MA 814485, MA814486, photo F neg. 29217). Figs. 2F, 3A, 6.

Distribution. Costa Rica, Colombia and Brasil to Ecuador and Peru. Expected in Panama.

Aspidosperma myristicifolium is distinguished by its channelled trunk, ferrugineous stems, leaf blades with brochidodromous venation, calyx 4-lobed, corolla lobes 6–8 mm, and follicles tomentose or tomentulose, without longitudinal ribs.

The specimen MA814484 is selected as the lectotype of *Geissospermum myristicifolium* because is the best preserved sheet and the only one with flowers.

Representative specimens examined. COSTA RICA. Puntarenas. Golfo Dulce, Rincón, 22 Oct 1993, *Morales et al. 1925* (CR, F, MO, NY, U, USJ). **San José**. Río Carara, 2 Apr 1993, *Gentry et al. 79279* (CR, MO).

7. ASPIDOSPERMA RIGIDUM Rusby, Mem. New York Bot. Gard. 7: 323. 1927. **TYPE: BOLIVIA. La Paz**. Bopi river, 12 Sep 1921, *Rusby 593* (holotype: NY 00297991). Figs. 2G, 5.

Aspidosperma jaunechense A.H. Gentry, Phytologia 4: 98. 1980. **TYPE: ECUADOR. Los Ríos**. Jauneche forest, km 70, Quevedo-Palenque via Mocachi, Canton Vinces, 26 Mar 1980, *Dodson & Gentry 9920* (holotype: MO; isotypes: QCNE 13, SEL 001170).

Distribution. Costa Rica to Brazil and Bolivia.

Aspidosperma rigidum is very distinctive by its deeply channelled trunk, leaf blades with brochidodromous venation, calyx 5-lobed, corolla tube 2.9–3.7 mm, lobes 5.5–6.8 mm, and follicles with longitudinal ribs, drying black.

Representative specimens examined. COSTA RICA. Puntarenas. Entre Guadoral y Colinas Miz de los Uvas, 20 Jul 1995, *Aguilar 4230* (CR, MO). **San José**. Turrubares, reserva biológica Carara, rio del Sur, desembocadura de la quebrada Chimarruda, 19 Apr 1995, *Zamora & Morales 2249* (CR, MO). **PANAMA. Los Santos**. Tonosi, Río Pedregal, 23 Apr 1968, *Holdridge 6236* (MO).
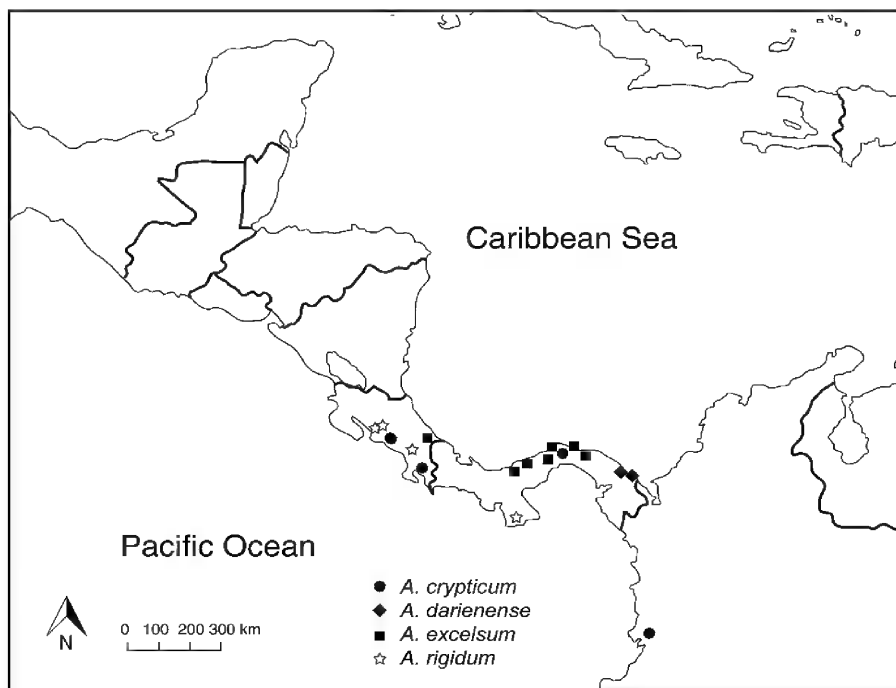
Figure 5. Distribution of *Aspidosperma crypticum*, *A. darienense*, *A. excelsum*, and *A. rigidum*.
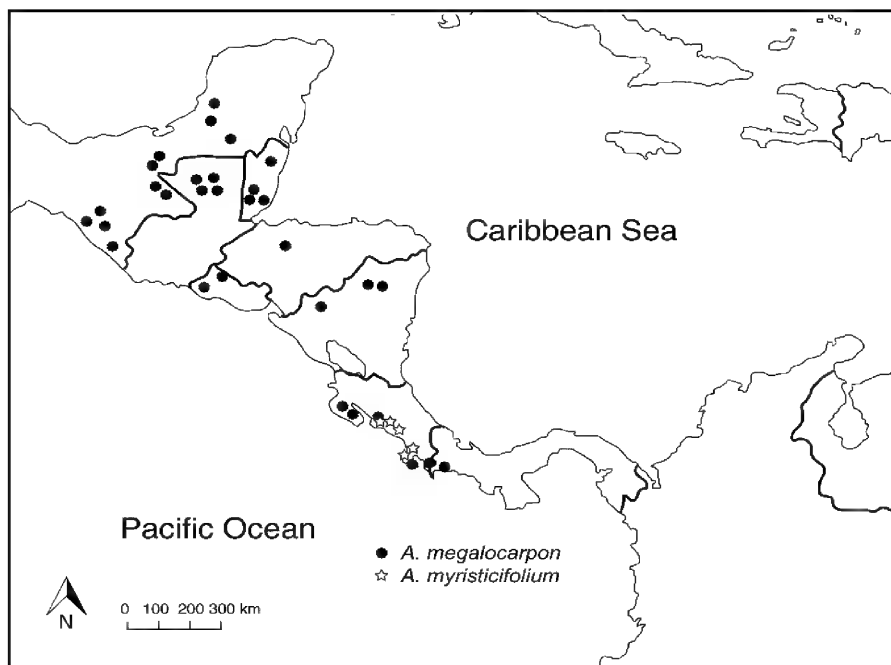
Figure 6. Distribution of *Aspidosperma megalocarpon* and *A. myristicifolium*.

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SURVEY OF HASKAMP WOODS, ALLEN COUNTY, INDIANA, AND FLORISTIC COMPARISON WITH NEIGHBORING FOREST PROPERTIES

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ABSTRACT

The vascular plant community was surveyed at Haskamp Woods, Allen County, Indiana, which we compared to six neighboring forests. We encountered 54 unique species across the understory, midstory, and overstory strata. Species richness and diversity at Haskamp Woods were greatest in the understory. Coefficient of conservatism at Haskamp Woods was only greater than one of the neighboring forests, while floristic quality index was the median value. Additionally, using nonmetric multi-dimensional scaling to visualize dissimilarity between the seven forests, Haskamp Woods was more dissimilar to the two properties with the longest protection history and the two privately owned properties. Overstory and midstory at Haskamp Woods were dominated by *Acer saccharum*. The overstory composition was relatively similar to five of the neighboring forests, with the sixth differing because it is an uncommon forest type in the region. Overall, Haskamp Woods had similarities and differences in species composition compared to the six neighboring forests. Variability in protection and disturbance histories, as well as edaphic conditions, result in variable forest communities.

In the Midwest United States, agriculture, including cultivated crops, pastureland, or other open-field agricultural practices, dominates the land cover types (Fry et al. 2011). Across the entire region, agriculture accounts for 60% of land use types. However, focusing on the southern half of the Midwest, cultivated and pastoral agriculture accounts for 80-90% of land use, with fragmentation of forests further driven by urban and suburban development (Radeloff et al. 2005). The majority of forests in the region are relatively small woodlots, most of which are privately owned (Fuelling 2014).

Forest fragments serve as important, suitable habitat for a wide range of organisms due to the often-unsuitable nature of surrounding matrix (Bouma et al. 2013). Influence by the surrounding matrix is variable depending on fragment isolation, quality of the matrix, and other underlying factors (Davies et al. 2000; Vandermeer & Carvajal 2001). This surrounding matrix is important as seed sources for plant community development through colonization and extinction processes (Fröborg & Eriksson 1997). Additionally, interactions between soil types and disturbance histories can lead to the development of uncommon forest types, which may differ from surrounding forests (Adkins et al. 2016).

Haskamp Woods is a 31.8 ha property that was privately owned until 2002, when it was purchased by the New Haven Parks and Recreation Department (pers. comm., A. Gurney). Over two-thirds of the property is currently cultivated row crop agriculture with 10.1 ha forested (pers. observ.). The forest canopy was patchy with large gaps visible in aerial images from 1938 and 1964, with canopy closure happing at some point after 1972 (IHAPI 2017a-c). Haskamp Woods is surrounded by privately owned land, which is a mixture of agriculture, forests, and suburban development. Close

proximity to agriculture and suburban development is typical for forest fragments within Indiana and the surrounding region (e.g. Brothers & Spingarn 1992; Fuelling 2014; Arvola et al. 2014; Adkins et al. 2016).

Understanding the baseline community composition and structure is important for development of sound management strategies. The objectives of this study were to conduct an ecological plant survey of understory, midstory, and overstory species in Haskamp Woods, Allen County, Indiana, and compare the plant community with neighboring forest properties. Results from this study regarding plant community composition, environmental variables, and forest structure will assist New Haven Parks and Recreation in making management decisions about Haskamp Woods.

MATERIALS AND METHODS

Study Design

Five transects were established at Haskamp perpendicular to the eastern edge of the property, with five plot centers along each transect 30 m apart (Figure 1). The eastern most plots were 33 m from the eastern edge of the property. At each plot center, two 1 m^2 understory quadrats were located
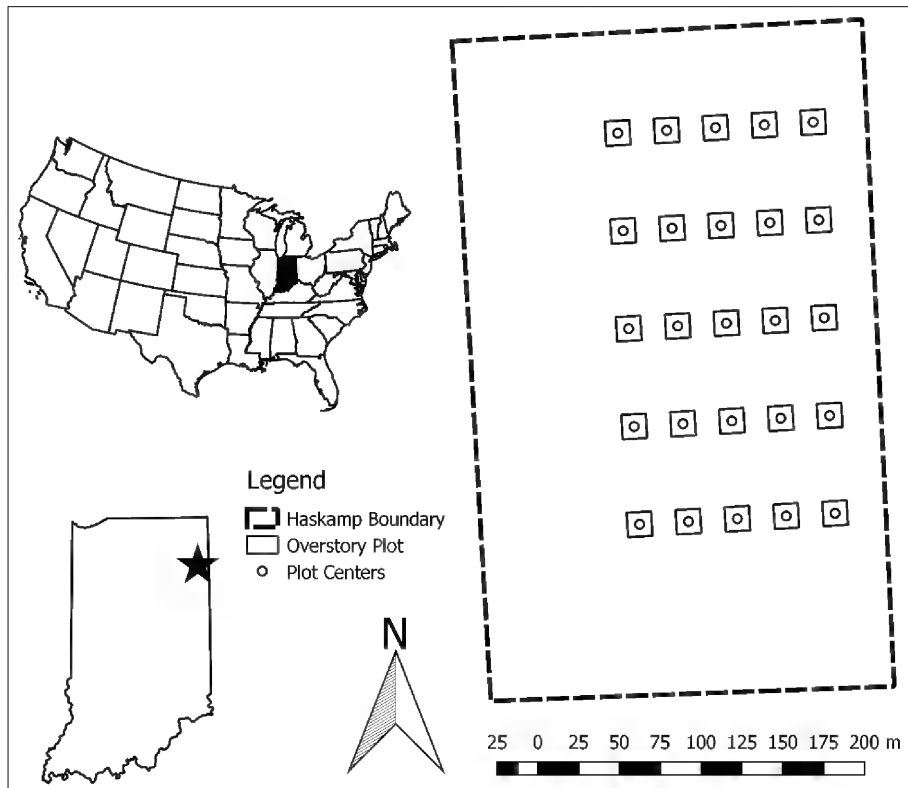

Figure 1. Study design in the forested portion of Haskamp Woods (location marked with star), Indiana, USA.

randomly within a 5 x 5 m area. A 10 x 10 m midstory plot and a 15 x 15 m overstory plot were established at each plot center. Mapping and spatial analyses were conducted in QGIS (version 2.18.3). Field data collection occurred 17-30 September 2016.

Plant Surveys

Within each 1 m^2 understory quadrat, all plants ≤ 2 m tall were counted and identified to species. Understory data was pooled at each plot center. Voucher specimens of understory plants were deposited in the Indiana University-Purdue University herbarium. Within each 100 m^2 midstory plot, all plants > 2 tall and ≤ 8 cm in diameter at breast height (dbh, 1.3 m above the soil surface) were counted and identified to species. Within each 225 m^2 overstory plot, all plants > 8 cm in dbh were counted, identified to species, and dbh was recorded. The largest diameter overstory individual in each plot was selected and two cores were collected at breast height, perpendicular to each other, with a 4.3 mm diameter increment borer (Haglöf Sweden AB, Långsele, Sweden). Cores were air dried, mounted on wood rails for support, progressively sanded with 220 to 500 grit sandpaper, and rings were counted.

Environmental Data

We measured percent volumetric soil moisture content, percent canopy cover, soil pH, litter depth, soil compaction, and percent available light at the corner of each 5 x 5 m, 10 x 10 m, and 15 x 15 m plot. Percent volumetric soil moisture content (VMC) was measured with a 12 cm long probe attached to a FieldScout TDR moisture meter (Spectrum Technologies Inc., Aurora, IL, USA). Percent canopy cover was measured with a concave spherical densiometer (Forestry Suppliers, Jackson, MS, USA). Soil pH was measured with a Fieldscout SoilStik meter (Spectrum Technologies Inc., Aurora, IL, USA). Litter depth was measured with a meter stick to the nearest 0.1 cm. Soil compaction was measured with a Lang penetrometer (Forestry Suppliers, Jackson, MS, USA) as insertion force (kgf). Percent available light was calculated from a six-sensor bar at each plot corner and an unattended single sensor (Spectrum Technologies Inc., Aurora, IL, USA) set outside of the forest in full sun. Light data was collected as μmol/m^2/sec of photons and converted to percent available light. Soil types and drainage information were defined by the USDA NRCS Web Soil Survey (http://websoilsurvey.sc.egov.usda.gov/) as the dominant values at the site.

Data Analysis

Species richness (S = number of species), Shannon's diversity index (H'=-Σp_i ln p_i, where p_i is the proportion of ith species in plot), and Pielou's evenness index (J'=H'/ln S) were calculated for understory, midstory, and overstory plants at each plot. Floristic Quality Index (FQI) was calculated for the property for understory species (FQI = C_{mean} x square root of the number of species, where C_{mean} is the mean coefficient of conservatism value for the entire property). Coefficient of conservatism values were attained from Rothrock (2004). Sørensen similarity index was calculated between midstory and overstory species (2 * number of shared species / sum of mistory and overstory richness). Overstory species relative importance values (RIV) were calculated as sum of relative frequency, relative dominance, and relative density. Relative frequency was calculated as frequency of species$_i$ / sum of all frequencies, where frequency of species$_i$ is the number of plots species$_i$ occurred / number of plots surveyed. Relative dominance was calculated as basal area of species$_i$ / sum of all basal areas, where basal area was the cross-sectional area of each species per ha calculated from dbh data. Relative density was calculated as density of species$_i$ / sum of all densities. We used RIV to determine the forest type of Haskamp Woods.

Haskamp Woods understory, midstory, and overstory compositions were compared to those of six neighboring forests in Allen County, Indiana (Figure 2). Detailed property descriptions can be found in their respective citations but are presented here briefly. **Fogwell Forest Nature Preserve** is a 12.3 ha state designated nature preserve owned and managed by ACRES Land Trust, which has
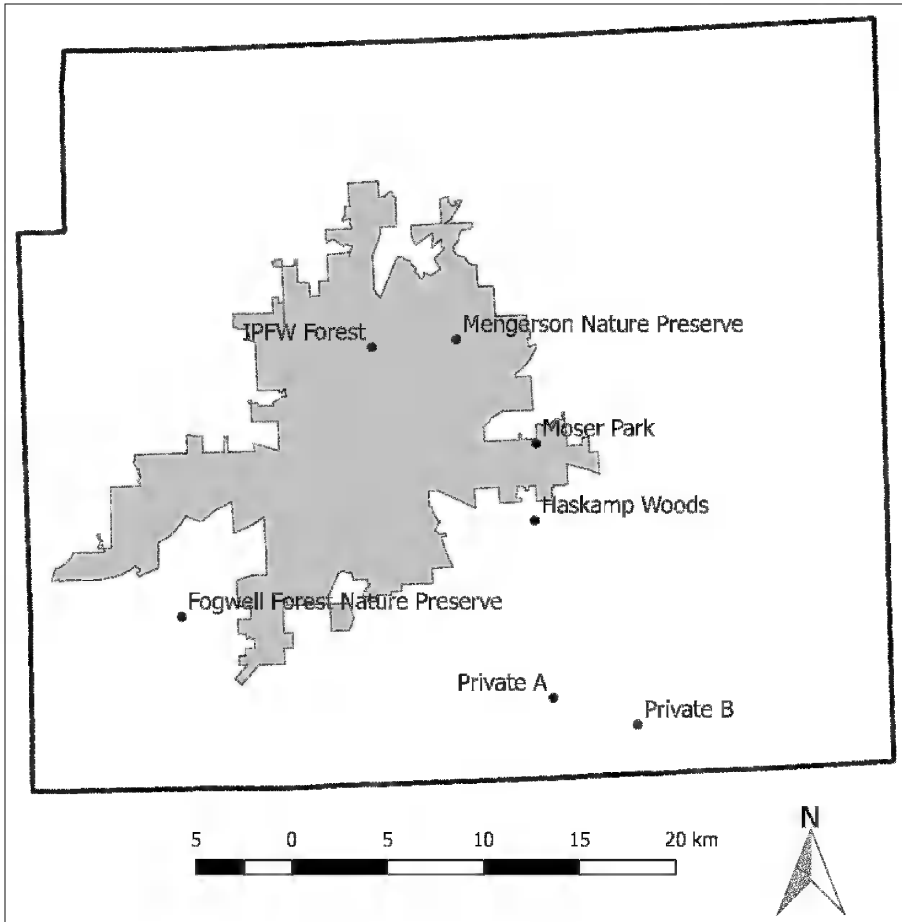
Figure 2. Geographic relationship between Haskamp Woods and six neighboring forests in Allen County, Indiana. Grey polygon represents City of Fort Wayne boundary.

been protected since the 1930s (Arvola et al. 2014). **Indiana University-Purdue University Fort Wayne (IPFW) forest** is a 13.8 ha forest adjacent to the university, which has been owned by IPFW since 2004 and does not have a formal protection status (Arvola et al. 2014). **Mengerson Nature Preserve** is a 14.4 ha state designated nature preserve owned and managed by ACRES Land Trust, which has been protected since 1973 (Arvola et al. 2016). **Moser Park** is a 5.6 ha forest managed by New Haven Parks and Recreation since 1962, which had previously been used for railroad storage and landings (Adkins et al. 2016). The two privately owned properties (**Private A** and **Private B**) were 10.4 ha and 6.7 ha, respectively (Fuelling 2014).

Plot means for each environmental data were calculated. Pearson correlation was used to identify relationships between environmental variables. We used non-metric multidimensional

scaling (NMDS) ordination to visualize relationships between understory communities in Haskamp and six neighboring forests, and environmental data (percent canopy cover and overstory richness), displayed as joint vectors. Understory species presence/absence values were used for the six properties from Adkins et al. (2016), Arvola et al. (2014), and Fuelling (2014). For NMDS, alternative Gower distances were calculated between communities. The alternative Gower distance excludes double-zeros between communities (Anderson et al. 2006). We used simple linear regression to relate understory and midstory species richness and diversity to the environmental variable mean values. Data analysis was conducted using base and Vegan packages in R (version 3.4.0, R Core Team 2017).

RESULTS

Three plots on the southern transect were omitted from the survey due to accessibility issues related to flooding. However, we were able to complete plant surveys at 22 plot center locations. We encountered 44 species in the understory, 18 in the midstory, and 20 in the overstory at Haskamp Woods (Appendix).

Mean percent canopy cover was high and relatively consistent throughout Haskamp (95.1% [SD = 3.5]), which resulted in low mean percent available light (7.2% [SD = 8.4]). Canopy cover and available light were negatively correlated ($r = -0.59$, $P = 0.004$). Mean percent volumetric soil moisture (18.5% [SD = 6.3]), pH (6.4 [SD = 0.3]), litter depth (2.9 cm [SD = 0.8]), and soil compaction (5.1 kgf [SD = 0.7]) were relatively more variable than canopy cover. Compaction and pH were positively correlated ($r = 0.51$, $P = 0.038$). Similarly, compaction and available light were positively correlated ($r = 0.48$, $P = 0.023$).

Understory richness was greater than the other two strata (Table 1). The most common understory plants were *Geum canadense* (Rosaceae) and *Fraxinus pennsylvanica* (Oleaceae), occurring in 20 and 16 of the plots, respectively. Additionally, these two species accounted for 51.6% of all individuals encountered in the understory. Fourteen species occurred only in one plot each. Additionally, six more species occurred in only two plots each. While mean coefficient of conservatism for Haskamp Woods was on the low end of the range of values at neighboring properties, FQI was the median for the values pooled (Table 2).

Distance between points in the NMDS plot represents dissimilarity in community compositions (i.e. points farther apart from each other are more dissimilar). It is important to note that in the NMDS plot, distance is in species-space and not in geographic space. Haskamp Woods was less dissimilar to IPFW Forest and Moser Park compared to the other properties. Direction of the joint vectors plotted over the NMDS ordination indicates the direction of influence on the understory communities (Figure 3). Similar to distance, direction in the NMDS plot is not related to geographic-space but is associated with the regression analysis between the plant community and the vector variable. The understory plant species presence and absence in Haskamp Woods was negatively influenced by percent canopy cover, although overstory species richness had minimal influence on the understory (Figure 3). Moser Park, which had a lower mean coefficient of conservatism and FQI compared to Haskamp Woods, was also influenced negatively by percent canopy cover (Figure 3).

Richness and diversity were lowest in the midstory (Table 1), which was skewed towards *Acer saccharum* (Sapindaceae) occurring in all plots and accounting for 65.8% of midstory individuals. The second most common midstory species, *Ostrya virginiana* (Betulaceae), accounted for only 10.5% of individuals. Seven midstory species occurred in only one plot and two additional species occurred in only two plots. Midstory diversity was positively related to percent light available ($r = 0.60$, $P = 0.003$) but was not related to soil moisture or compaction. Haskamp Woods shared relatively few species with the six neighboring forests (Table 3). The other forests had fewer total species compared to Haskamp Woods (range = 5-12, mean = 8.2, SD = 3.1).
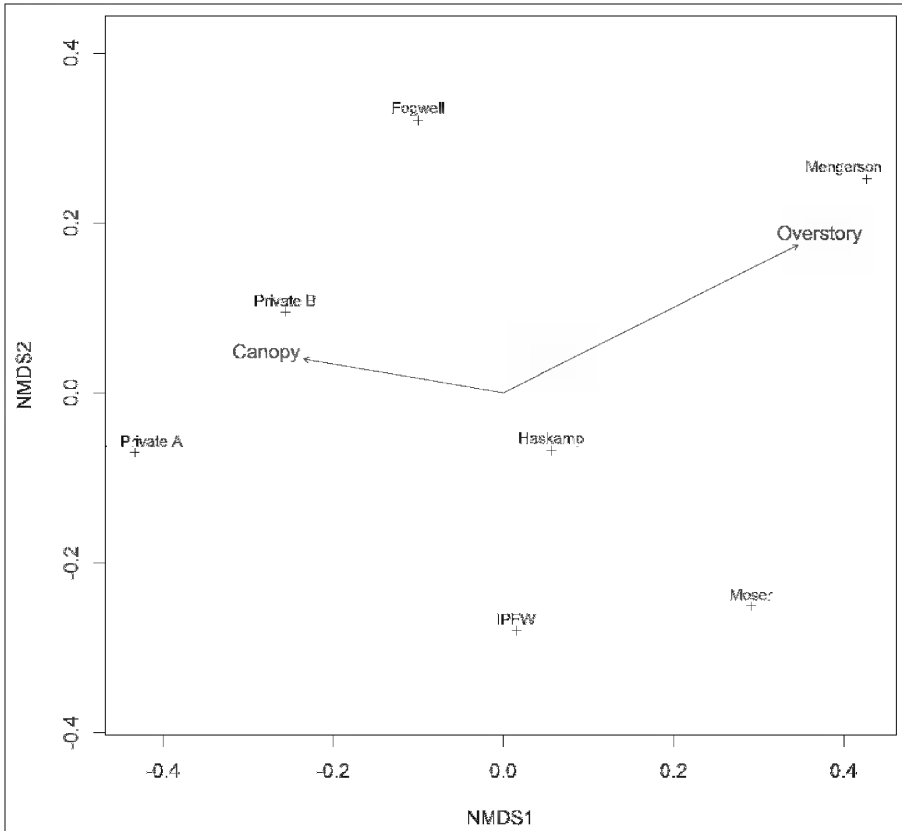
Figure 3. Nonmetric multi-dimensional scaling (NMDS) ordination of understory species presence and absence in Haskamp Woods and six neighboring forests. Joint vectors represent mean percent canopy cover (Canopy) and overstory species richness (Overstory) in each forest.

In the overstory, *Acer saccharum* was also the most common species accounting for 34.8% of individuals. Additionally, similar to the midstory, *Ostrya virginiana* was the second most common accounting for 21.8% of individuals. Because of the high frequency, dominance, and density, *A. saccharum* was the highest ranked species in relative importance value in the overstory, which aligned with a Sugar Maple forest type (Table 4). Seven overstory species occurred only in one plot and two species occurred in only two plots. Overstory and midstory strata were relatively similar (Sørensen similarity index = 0.74). Haskamp Woods overstory composition was more similar to the six neighboring forests than the midstory (Table 3). Additionally, there was a relatively similar number of species in those six forests compared to Haskamp Woods (range = 14-25, mean = 17.8, SD = 4.2). Overstory at 4 of the neighboring forests (Fogwell, IPFW, Mengerson, Private B) was also dominated by *A. saccharum*. While the other private property aligned more with a Beech-Maple forest type, it was still relatively similar to Haskamp Woods (Table 3). Moser was the least similar because of the different forest type, which was dominated by *Celtis occidentalis*, *Ulmus americana*,

and *Fraxinus pennsylvanica* (Table 3). The median age of the largest diameter overstory individual in each plot was 43.5 years, with a range of 25 to 125 years.

Table 1. Mean richness, Shannon's diversity index, and Pielou's evenness index (standard error) for understory, midstory, and overstory plant community strata in Haskamp Woods calculated from plot level values.

Stratum	Richness	Diversity	Evenness
Understory	8.41 (0.59)	1.37 (0.10)	0.66 (0.05)
Midstory	3.95 (0.62)	0.77 (0.14)	0.65 (0.05)
Overstory	4.41 (0.31)	1.14 (0.09)	0.79 (0.03)

Table 2. Understory mean coefficient of conservatism (C_{mean}), floristic quality index (FQI), dominant soil type, and drainage description for Haskamp Woods and six neighboring properties in Allen County, Indiana. Values for Fogwell Forest Nature Preserve, IPFW Forest, and Mengerson Nature Preserve from Arvola et al. (2014). Values from Moser Park from Adkins et al. (2016). Private property values from Fuelling (2014).

Property	C_{mean}	FQI	Soil Type	Drainage
Fogwell Forest Nature Preserve	4.1	23.4	Blount Silt Loam	Somewhat Poor
Haskamp Woods	3.1	20.2	Glynwood Silt Loam	Moderately Well
IPFW Forest	3.4	18.6	Glynwood Silt Loam	Moderately Well
Mengerson Nature Preserve	3.6	18.9	Blount Silt Loam	Somewhat Poor
Moser Park	2.7	15.9	Eel Silt Loam	Moderately Well
Private Property A	4.4	26.3	Pewamo Silt Loam	Very Poor
Private Property B	4.2	25.3	Pewamo Silt Loam	Very Poor

Table 3. Sørensen similarity index values for midstory and overstory species between Haskamp and six neighboring forest properties in Allen County, IN, with forest types. Values for Fogwell Forest Nature Preserve, IPFW Forest, and Mengerson Nature Preserve from Arvola et al. (2014). Values from Moser Park from Adkins et al. (2016). Private property values from Fuelling (2014).

	Fogwell	IPFW	Mengerson	Moser	Private A	Private B
Midstory	0.33	0.54	0.47	0.33	0.33	0.26
Overstory	0.65	0.52	0.57	0.33	0.53	0.59

DISCUSSION

Haskamp Woods is a 10.1 ha forested property owned and managed by New Haven Parks and Recreation that is centrally located in Allen County, Indiana. Like many small forests in the region, it is surrounded by cultivated row-crop agriculture and suburban development. The dominant soil type at Haskamp Woods is derived from glacial moraines, which is common for the region, and the subsequent forest type that has developed at this site is an *A. saccharum* dominated forest type, common in the region (Gray 2000; Homoya et al. 1985). While the forest type may be common, the importance of Haskamp Woods is in the limited forest cover in the region.

Over the last four decades, canopy closure has occurred from large patchy gaps in 1972 to 95% canopy cover in 2016 (IHAPI 2017c). In the historic aerial photos from 1938-1972, these gaps remained visible and likely are the result of selective harvesting by previous land owners (IHAPI 2017a-c). The median age of 43.5 years calculated for the forest aligned with potential canopy

closure beginning in the early to mid-1970s. New Haven Parks and Recreation has owned the property since only 2002, so the owner prior to this most recent sale removed few trees allowing the canopy to close. As would be expected –– as canopy cover increased light availability decreased. The positive relationship between compaction and available light is likely due to old two-track and single-track paths in Haskamp Woods, some of which were apparent.

The two most common understory species (*Geum canadense* and *Fraxinus pennsylvanica*) both had a coefficient of conservatism value of 1 (Rothrock 2004). Coefficient of conservatism values 0 to 3 are assigned to species that are highly tolerant of disturbance and provide little to no indication of undisturbed habitat (Rothrock 2004). Only one species in the community, *Circaea alpina*, fit the coefficient of conservatism value range of 9 to 10 (indicating species restricted to remnant habitat with very little post-settlement disturbance; Rothrock 2004), in three plots in the southwest corner. Even though Haskamp Woods has reached closed canopy status, the understory is dominated by species that tolerate disturbance. This dominance of the understory by disturbance tolerant species is why Haskamp Woods was the least dissimilar from IPFW and Moser in the NMDS ordination. Moser also had high frequency of low coefficient of conservatism value species due to intense disturbance history (Adkins et al. 2016). Additionally, IPFW was also dominated by low coefficient of conservatism value species and has a relatively recent protection history (Arvola et al. 2014).

Domination of the midstory stratum by *Acer saccharum* is not unusual for the site or the region. Considering the overstory domination by this species and time since major disturbances, Haskamp Woods likely is progressing through the understory reinitiation stage of stand development (Oliver and Larson 1996). The relatively few *A. saccharum* individuals in the understory (10% of understory individuals) and relatively large number of *A. saccharum* in the midstory (>65% of midstory individuals) suggest that many of the early individuals to establish during the reinitiation stage have progressed into subsequently larger size classes (i.e. grown from understory to midstory). Progression from understory reinitiation to later stages of stand development is variable and difficult to predict (Oliver & Larson 1996). Shade-tolerant species like *A. saccharum* have the ability to "wait for release" and respond to gap formation following long-term suppression (Canham 1985). Since Haskamp Wood canopy has closed (95% canopy cover), *A. saccharum* will continue to dominate the midstory as the stand ages. This will likely lead to continued dominance of *A. saccharum* in the overstory as gaps form and those midstory individuals are released into the canopy.

Based on the high RIV ranking of *Acer saccharum* in the overstory, Haskamp Woods fits the Sugar Maple forest type (Eyre 1980). While Black Cherry-Maple is a defined forest type and *Prunus serotina* was third ranked in RIV, Haskamp Woods did not align with this type; second ranking of *Ostrya virginiana* and lower relative dominance of *P. serotina* align better with the Sugar Maple type. This forest type, along with other types co-dominated by *A. saccharum,* are common throughout this region (Gray 2000; Homoya et al. 1985). The similarity in overstory species composition between Haskamp Woods and five of the neighboring forests is expected due to the prevalence of *A. saccharum* forest types in the region.

Evidence of past disturbance is still present in Haskamp Woods (i.e. relatively low C_{mean}, visible remnants of two-track paths). However, the forest has progressed through developmental stages (i.e. canopy closure since 1970s, well established midstory tree community). There are clear similarities and differences in species composition when comparing Haskamp Woods to neighboring forests. If Haskamp Woods is allowed to progress naturally through succession, it will likely continue to be dominated by *A. saccharum*. Active management by New Haven Parks and Recreation could increase the speed that certain species are lost from the overstory stratum and are replaced by midstory *A. saccharum*. This would add to the unique disturbance history experienced by Haskamp Woods.

Table 4. Frequency (number of plots), basal area (m^2/ha), density (individuals/ha), and rank order of relative importance values (RIV) for overstory species encountered in Haskamp Woods.

Species	Frequency	Dominance	Density	RIV Rank
Acer rubrum	3	0.82	22.22	8
Acer saccharum	20	5.00	238.38	1
Aesculus glabra	1	0.01	2.02	20
Carya cordiformis	1	0.04	2.02	16
Carya ovata	1	0.65	2.02	13
Carya tomentosa	2	0.18	12.12	12
Celtis occidentalis	4	0.46	16.16	9
Fagus grandifolia	5	1.20	12.12	7
Fraxinus pennsylvanica	1	0.03	2.02	18
Gleditsia triacanthos	1	0.01	2.02	19
Juglans nigra	2	0.17	4.04	14
Ostrya virginiana	16	1.66	149.49	2
Populus grandidentata	2	0.74	10.10	10
Prunus serotina	11	2.05	123.23	3
Quercus alba	3	2.91	6.06	6
Quercus rubra	7	2.09	40.40	4
Quercus velutina	1	0.03	2.02	17
Ulmus americana	11	0.92	28.28	5
Ulmus rubra	4	0.16	8.08	11
Ulmus thomasii	1	0.05	2.02	15

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Appendix. Annotated list of vascular plants encountered in Haskamp Woods, Allen County, Indiana.

Nomenclature follows ITIS (2017). Taxa are arranged alphabetically by family, genus, and specific epithet. Species followed by an asterisk (*) after authority name are considered non-native based on USDA NRCS (2017). Herbarium collection numbers [in brackets] listed for those understory species with voucher specimens deposited in Indiana University-Purdue University Fort Wayne, Department of Biology herbarium. Relative abundance is listed for each species as Rare (one

or two occurrences), Occasional (sporadic occurrence), Frequent (widespread throughout plant community), or Common (dominants in the plant community). Understory were individuals ≤ 2 m tall, midstory were > 2 m tall and ≤ 8 cm in diameter at breast height (dbh, 1.3 m above the soil surface), and overstory were > 8 cm dbh.

Adoxaceae
Viburnum prunifolium L. [*HW15*] - Understory (Occasional)

Anacardiaceae
Toxicodendron radicans (L.) Kuntze - Understory (Occasional)

Aristolochiaceae
Asarum canadense L. [*HW31*] - Understory (Rare)

Asparagaceae
Maianthemum racemosum (L.) Link [*HW19*] - Understory (Occasional)

Asteraceae
Ambrosia trifida L. [*HW05*] - Understory (Rare)
Symphyotrichum sp. [*HW34*] - Understory (Rare)

Betulaceae
Carpinus caroliniana Walter - Midstory (Rare)
Ostrya virginiana (Mill.) K. Koch [*HW12*] - Understory (Frequent), Midstory (Frequent), Overstory (Common)

Brassicaceae
Alliaria petiolata (M. Bieb.) Cavara & Grande* [*HW30*] - Understory (Rare)

Cannabaceae
Celtis occidentalis L. [*HW41*] - Understory (Rare), Midstory (Rare), Overstory (Occasional)

Caprifoliaceae
Lonicera maackii (Rupr.) Herder* [*HW37*] - Understory (Occasional), Midstory (Rare)

Celastraceae
Euonymus americanus L. [*HW40*] - Understory (Rare)

Cyperaceae
Carex sp. L. - Understory (Rare)

Fabaceae
Gleditsia triacanthos L. - Overstory (Rare)

Fagaceae

Fagus grandifolia Ehrh. [*HW28*] - Understory (Rare), Midstory (Occasional), Overstory (Occasional)

Quercus alba L. [*HW11*] - Understory (Rare), Overstory (Occasional)

Quercus rubra L. [*HW26*] - Understory (Occasional), Midstory (Rare), Overstory (Occasional)

Quercus velutina Lam. - Overstory (Rare)

Grossulariaceae

Ribes cynosbati L. [*HW38*] - Understory (Rare)

Juglandaceae

Carya cordiformis (Wangenh.) K. Koch [*HW06*] - Understory (Occasional), Midstory (Occasional), Overstory (Rare)

Carya ovata (Mill.) K. Koch [*HW18*] - Understory (Occasional), Midstory (Rare), Overstory (Rare)

Carya tomentosa (Lam. ex Poir.) Nutt. - Midstory (Rare), Overstory (Rare)

Juglans nigra L. - Overstory (Rare)

Menispermaceae

Menispermum canadense L. [*HW35*] - Understory (Rare)

Oleaceae

Fraxinus americana L. [*HW21*] - Understory (Rare), Midstory (Occasional)

Fraxinus pennsylvanica Marsh. [*HW07*] - Understory (Common), Midstory (Occasional), Overstory (Rare)

Onagraceae

Circaea alpina L. [*HW39*] - Understory (Occasional)

Oxalidaceae

Oxalis stricta L. [*HW33*] - Understory (Rare)

Poaceae

Unidentified species - Understory (Occasional)

Polygonaceae

Persicaria virginiana (L.) Gaertn. [*HW13*] - Understory (Occasional)

Primulaceae

Lysimachia nummularia L. [*HW44*] - Understory (Rare)

Ranunculaceae

Thalictrum thalictroides (L.) Eames & B. Boivin [*HW42*] - Understory (Rare)

Rosaceae

Crataegus mollis Scheele [*HW25*] - Understory (Rare)

Fragaria virginiana Duchesne [*HW29*] - Understory (Rare)

Geum aleppicum Jacq. [*HW24*] - Understory (Occasional)
Geum canadense Jacq. [*HW02*] - Understory (Common)
Geum laciniatum Murray [*HW20*] - Understory (Rare)
Malus coronaria (L.) Mill. - Midstory (Rare)
Prunus serotina Ehrh. [*HW14*] - Understory (Occasional), Midstory (Occasional), Overstory (Frequent)
Rosa multiflora Thunb.* [*HW10*] - Understory (Occasional), Midstory (Rare)
Rubus allegheniensis Porter [*HW17*] - Understory (Occasional)

Rubiaceae
Galium aparine L. [*HW22*] - Understory (Rare)

Salicaceae
Populus grandidentata Michx. - Overstory (Rare)

Sapindaceae
Acer rubrum L. [*HW27*] - Understory (Occasional), Overstory (Occasional)
Acer saccharum Marsh. [*HW03*] - Understory (Frequent), Midstory (Common), Overstory (Common)
Aesculus glabra Willd. - Midstory (Rare), Overstory (Rare)

Smilacaceae
Smilax tamnoides L. [*HW16*] - Understory (Occasional)

Ulmaceae
Ulmus americana L. [*HW08*] - Understory (Occasional), Midstory (Occasional), Overstory (Frequent)
Ulmus rubra Muhl. - Overstory (Occasional)
Ulmus thomasii Sarg. - Overstory (Rare)

Urticaceae
Boehmeria cylindrica (L.) Sw. [*HW32*] - Understory (Rare)

Violaceae
Viola sororia Willd. [*HW09*] - Understory (Occasional)

Vitaceae
Parthenocissus quinquefolia (L.) Planch [*HW04*] - Understory (Occasional)
Vitis riparia Michx. [*HW23*] - Understory (Frequent)

ADELONEMA PELTATUM (ARACEAE), A NEW RECORD FOR THE FLORA OF PANAMA

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ABSTRACT

We present the first record of *Adelonema peltatum* for Panama and Central America. Images of the species, taxonomic comments, and a key for Panamanian *Adelonema* are provided.

RESUMEN

Presentamos el primer registro de *Adelonema peltatum* para Panamá y Centroamérica. Se proporcionan imágenes de la especie, comentarios taxonómicos, y una clave para las especies panameñas de *Adelonema*.

We record the species *Adelonema peltatum* (Mast.) Wong & Croat for the first time for Panama and Central America, bringing to six the number of *Adelonema* species reported for Panama. Additionally, a key of the Panamanian *Adelonema* species is provided.

Adelonema peltatum (Mast.) S.Y. Wong & Croat, Syst. Bot. 41: 43. 2016. Figures 1–3.
　　Homalomena peltata Mast., Gard. Chron., n. ser. 7: 273. 1877. **TYPE: Colombia**. Cultivated by Bull, ex. Shuttleworth, *Masters s.n.* (holotype: K!).

　　Distribution. Panama (Comarca Guna Yala), Colombia (Antioquia) to Ecuador.

　　Panama specimen examined. Comarca Guna Yala (San Blas). Forest SE of Puerto Obaldía on steep creek bank, 08°39'30"N 077°23'18"W, 18 Aug 1971, *Croat & Gentry 16811* (MO). The plant was collected in a Tropical wet forest life zone at ca. 150 m.

　　Notes. *Adelonema peltatum* (sect. *Curmeria*) is characterized mainly by having peltate blades usually with the blades forming a deep depression owing to the fusion of the upturned margins and upturned posterior lobes with the upper surface usually weakly glossy to matte on drying with spinose petioles with the surfaces usually densely puberulent to hispidulous throughout or at least toward the apex (see the key below). In Panama, *A. peltatum* can be confused with *A. panamense*, since both species have peltate blades and spines on the petioles. *Adelonema panamense* differs from *A. peltatum* in having leaf blades glossy and glabrous on upper surface with posterior lobes flat.

Figure 1. Voucher for Panama occurrence of *Adelonema peltatum, Croat & Gentry 16811* (MO). Photo credits: © MO Herbarium.
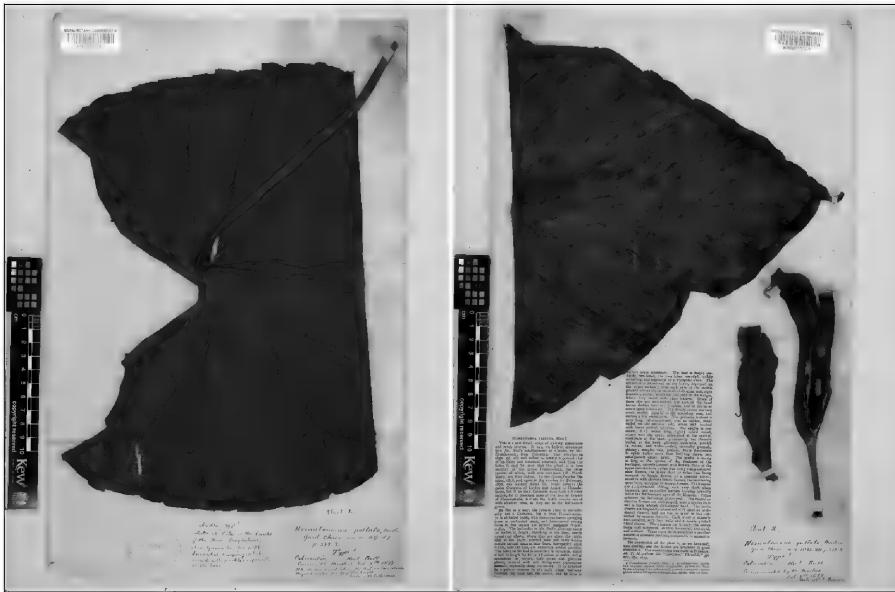
Figure 2. Type of *Homalomena peltata* Masters, *Masters s.n.* (K). Photo © copyright of the Board of Trustees of the Royal Botanic Gardens, Kew.

Figure 3. Original illustrations of *Homalomena peltata* Masters. From Masters (1877): figures 45 and 46.

Key to *Adelonema* species of Panama (based on Wong et al. 2016)

1. Leaf blades broadly to narrowly ovate or elliptic, base not lobed, without trichomes or spines.

    5. Petioles short, 1.5–4(–6.5) cm long, sheath usually extending nearly to blade
    .... **Adelonema wallisii**
    5. Petiole over 6.5 cm long, sheath usually extending to no more than about mid-petiole
    .... **Adelonema allenii**

1. Leaf blades cordate to hastate, base evidently lobed with trichomes, those on petiole sometimes much thickened and spinescent.

    2. Petioles sulcate, densely to slightly pubescent with filamentous trichomes, especially near apex, but never with spines .... **Adelonema picturatum**
    2. Petioles terete or nearly so, usually with spinose trichomes towards base.

        3. Leaf blades basifixed .... **Adelonema wendlandii**
        3. Leaf blades peltate at base.

            4. Blades glossy and glabrous on upper surface, posterior lobes flat; midrib and proximal portion of primary lateral veins pale green to whitish .... **Adelonema panamensis**
            4. Blades usually matte and obscurely puberulent on upper surface; posterior lobes directed prominently upward at an angle to midrib; midrib and primary lateral veins concolorous to pale green .... **Adelonema peltatum**

      Adelonema is a Neotropical genus of Araceae characterized as either mesophytic, helophytic, or rheophytic terrestrial herbs; petiolar sheath well-developed; leaves lanceolate, elliptic, oblong, subtriangular or cordate to sagittate, rarely peltate; ovules anatropous; placentation central; petiole often armed with prickles and leaf blade glabrous or pubescent, often variegated (Wong et al. 2016).

      The genus *Adelonema* was long-considered synonymous with *Homalomena* (Mayo et al. 1997). Traditionally, several studies argued that *Homalomena* was a polyphyletic group, with distinct Neotropical species and Asian species. Recently, molecular studies (nuclear ITS and plastid matK regions) (Wong et al. 2014) resurrected the genus *Adelonema* as distinct from the Asian *Homalomena*. The taxon *Adelonema* currently consists of 16 strictly Neotropical species in two distinct sections: **sect. *Adelonema*** with 10 species: *A. erythropus* Schott, *A. allenii* (Croat) S.Y. Wong & Croat, *A. hammelii* (Croat & Grayum) S.Y. Wong & Croat, *A. kvistii* (Croat) S.Y. Wong & Croat, *A. moffleriana* (Croat & Grayum) S.Y. Wong & Croat, *A. orientalis* Croat, *A. palidinervia* Croat, *A. roezlii* (Mast.) S.Y. Wong & Croat, *A. speariae* (Bogner & Moffler) S.Y. Wong & Croat, and *A. wallisii* (Regel) S.Y. Wong & Croat; and **sect. *Curmeria*** with six species: *A. crinipes* (Engl.) S.Y. Wong & Croat, *A. panamensis* Croat & Mansell, *A. peltatum* (Mast.) S.Y. Wong & Croat, *A. picturatum* (Linden & André) S.Y. Wong & Croat, *A. wendlandii* (Schott) S.Y. Wong & Croat, and *A. yanamonoensis* Croat & Mansell. Sect. *Curmeria* is characterized by having petioles often armed with prickles, leaf blades pubescent, spadix stipitate and interpistillar staminodes sometimes present. Sect. *Adelonema* is characterized by having petioles not armed, leaf blades glabrous, spadix sessile and interpistillar staminodes always absent (Wong et al. 2016).

ACKNOWLEDGEMENTS

peltatum. The first author of this paper (O.O.O.) thanks Panama's National Secretariat for Science and Technology (SENACYT) for funding the herbarium work. Lastly, we offer thanks to Jerry Harrison for his suggestions and comments.

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NEW RECORDS OF VASCULAR PLANTS FOR KANSAS

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ABSTRACT

Three new state records of vascular plants are reported for Kansas, including *Cenchrus atropurpuroides* from Crawford County, *Carex atherodes* from Johnson County, and *Spiraea prunifolia* from Neosho County. The latter two are older collections from (respectively) 1967 and 1995.

Recent fieldwork regionally by the author (mostly in Kansas and Oklahoma) and routine curatorial work in the T.M. Sperry Herbarium (KSP) at Pittsburg State University is revealing a steady stream of county records and even state records (e.g., Snow et al. 2017). The author presently reports most county records (including voucher information) to the BONAP's *Floristic Synthesis of North America* (Kartesz 2017). The following three species appear to represent state records for Kansas. The KSP numbers refer to barcode numbers of the specimens.

Cenchrus atropurpuroides (L.) Thunb.
Kansas. Crawford Co.: Pittsburg, Centennial Drive, ca. 80 m E of intersection with S. Joplin St., 27°22'56.00" N, 94°41'58" W (WGS84) +/- 5 m, elev. 277 m, N side of street on edge of lawn and sidewalk, Oct 2016, *Snow 10980* (KSP 011502).

This species is a widely cultivated, non-native ornamental, commonly called "Chinese fountain grass." It is planted in several places on the Pittsburg State University campus, approximately 0.8 km to the north of the collection locality, and used in landscaping in many other sites regionally.

Only one inflorescence was noted as emerging from the relatively well maintained (and mown) lawn at the time of collecting. However, a year later (October 2017) an inflorescence of the same species was emerging along the same lawn along the same stretch of sidewalk. Dr. Gerrit Davidse (MO) confirmed the identification of the specimen and indicated that the species is also becoming adventive locally in St. Louis, Missouri.

Based on data from Kartesz (2017), the nearest confirmed adventive collections (to the north and east) are in Johnson Co., Missouri, to the south in Pulaski Co., Arkansas, and west in Larimer Co., Colorado.

Carex atherodes Spreng.
Kansas. Johnson Co.: 35 mi SW [of] Mission, 22 Jun 1967, *Standley 519* (KSP 006088). The collection label indicates only "bog" as habitat. The specimen matches the description for the species in *Flora of North America* (Reznicek & Catling 2002) and was compared to specimens at the Missouri Botanical Garden in 2016.

Commonly called "Wheat sedge," the nearest collection of this native species is in neighboring Jackson Co., Missouri (Kartesz 2017). The nearest collection north (and somewhat west) is Nemaha Co., Nebraska. The native range of the species in the USA spans Washington to Maine and Virginia and south to California and New Mexico.

Spiraea prunifolia Sieb. & Zucc.

Kansas. Neosho Co.: St. Paul, ¼ mi N of St Francis Catholic Church, 8 Apr 1995, *Holland 8290* (KSP 006394). The label indicates that the specimen was "established on a roadside bank," but I have not confirmed that the population is still extant.

This shrubby ornamental species is known as "Bridal wreath." It is reported in Texas from Madison County and occurs sporadically east of there in most states. The greatest number of county records (Kartesz 2017) are from Arkansas, Missouri, Virginia, and southern New Jersey. The nearest two collections to the Kansas collection are in Newton (to the southeast) and Johnson counties (to the northeast) in Missouri.

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SPIRANTHES OVALIS VAR. *EROSTELLATA* (ORCHIDACEAE) NEW TO NEW YORK

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ABSTRACT
Spiranthes ovalis var. *erostellata* (Orchidaceae) is reported for the first time in New York State. First collected in 2015 and originally misidentified, it was rediscovered at the same site in 2017 and correct identification confirmed. This finding expands its known range by over 500 km to the north and by nearly 700 km to the east. This late-flowering native species was discovered in a disturbed habitat, and may be overlooked in other locations.

We report the first confirmed record of *Spiranthes ovalis* var. *erostellata* (Orchidaceae) for New York State. This is the most northern and eastern record known for this native species (Sheviak & Brown 2002).

Spiranthes ovalis Lindley var. **erostellata** Catling
New York. St. Lawrence Co.: Town of Massena, adjacent to the Wiley Dondero Canal of the St. Lawrence River, 220 m SE of Robinson Bay Rd, 2.4 km E of Barnhart Island Rd, 44.98540 N 74.81661 W, 122 m elev, 16 Sep 2017, *Daniel and Johnson s.n.* (BH).

Spiranthes ovalis var. *erostellata*, oval ladies tresses or October ladies tresses, a member of the *Spiranthes cernua* complex (Pace & Cameron 2016), is known from the southeastern to the upper midwestern USA and southwestern Ontario. We found it in extreme northern New York, a location over 500 km north-northeast of the closest confirmed record in central Pennsylvania and nearly 700 km northeast from the nearest known record in southwestern Ontario, on Walpole Island.
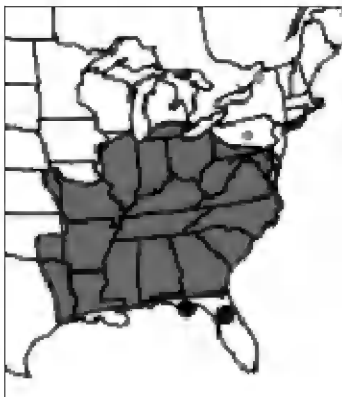

Figure 1. Distribution of *Spiranthes ovalis* var. *erostellata*. Modified from Sheviak and Brown (2002) to include records (red circles) from central Pennsylvania and the recent record from New York.

Throughout most of its northern range *Spiranthes ovalis* var. *erostellata* is considered a rare or uncommon species. It is listed as S1 (critically endangered) in Ontario (Oldham & Brinker 2009), where it was first found in 1985 (Brown 1986). Michael Oldham, Botanist for the Ontario Natural Heritage program, has records from four sites, but he is not aware of any reports in the province in more than a decade (Oldham, pers. comm.). It is not ranked in Michigan (Natureserv 2017), where there are records from five counties, all in the southern part of the state (Michigan Flora Online 2017). It is ranked S1 in Pennsylvania (Natureserv 2017), with five records. In addition to a 1961 collection in Franklin County in south-central Pennsylvania (Pennsylvania Flora Project 2017), the Carnegie Museum of Natural History has four herbarium collections, two from Greene County in southwestern Pennsylvania, made in 2003 and 2005 (Consortium of Midatlantic Herbaria Data Portal 2017), and two 1996 collections from Blair and Huntingdon counties in central Pennsylvania (Consortium of Midwest Herbaria Data Portal 2017). Further afield there have been several recent collections in the Chicago region (Wilhelm & Rericha 2017) and it was recently reported from southeastern Wisconsin, where it is ranked S1 (NatureServ 2017; Carter & Pace 2013). Published reports suggest that it is expanding its range (Wilhelm & Rericha 2017; Homoya 1993; Brown et. al 1987; Sheviak 1974).

Figure 2. Habitat of *Spiranthes ovalis* var. *erostellata* adjacent to the Wiley Dondero Canal of the St. Lawrence Seaway, near Massena, New York. Photo by S. Daniel.

In September 2015 we found a small population of this species at a site near the St. Lawrence Seaway in northern New York. We puzzled over it extensively and mistakenly called it *Spiranthes casei,* a species known from New York but not one familiar to the authors. At that time we did not consider *S. ovalis* as a possibility, possibly blinded by the fact that it was so far out of its known range. In August 2017 we found what we determined to be good *S. casei.* We strongly suspected, due to differences of phenology, flower structure, and habitat that what we had seen in 2015 was a different taxon altogether. We returned to the site on September 16, 2017, while leading a botany

field trip. After a search, one of the participants found four plants, which led to our finding a total of seven flowering stems in a small area. Close inspection of it revealed that this was *S. ovalis* var. *erostellata*. We sent pictures to A.A. Reznicek, curator of the University of Michigan Herbarium, who confirmed the identification.

Var. *erostellata*, described in 1983, is more common than var. *ovalis*, differing from it in the lack of a viscidium and rostellum, thus not being insect pollinated but instead self-pollinated or autogamous (Catling 1983). It was this character, along with the very small (less than 5 mm long flowers), that helped us confirm the identification. Note the absence of viscidium and rostellum in the photo.
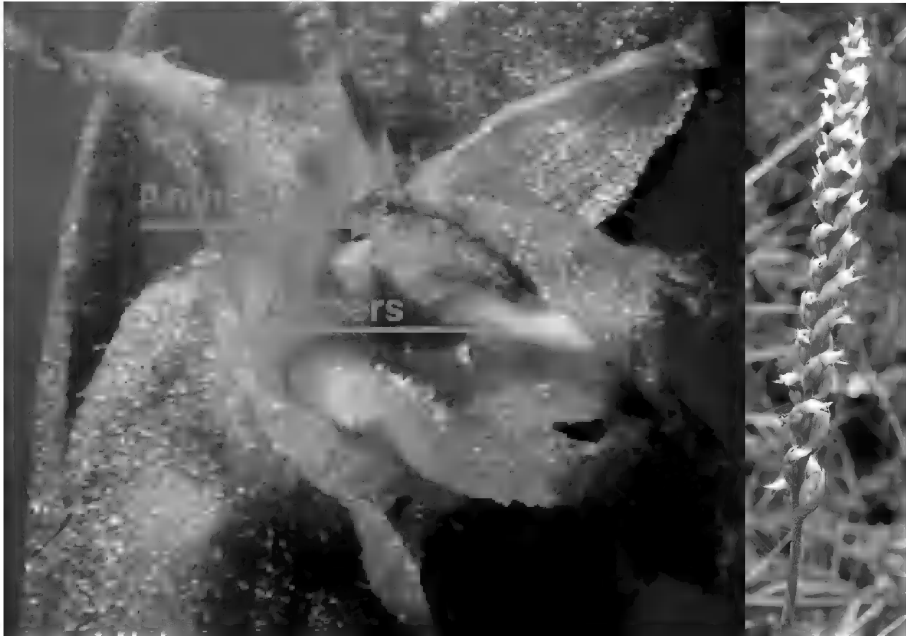
Figure 3. *Spiranthes ovalis* var. *erostellata*. Left: opened flower –– note lack of viscidium and rostellum. Right: inflorescence. Photos by S. Daniel.

While the habitat for this species has been described as open woodland or oak savanna, often on thin, calcareous soils, in Ontario it has been found in wet-mesic prairie (Brown et al 1987). It has also been found in disturbed habitats, including old fields, ditches, and on fill (Wilhelm & Rericha 2017).

The site where we found *Spiranthes ovalis* var. *erostellata* is adjacent to the Wiley Dondero Canal of the St. Lawrence Seaway. It grows there on fill –– dry, calcareous, clayey, dredge spoil from the construction of the St. Lawrence Seaway in the 1950's (Soil Survey Staff 2017). The habitat was somewhat open with low-growing herbaceous plants and a few scattered trees and shrubs nearby. The places we found the most plants tended to lack high density competition from other species.

After the initial discovery of 7 flowering stems on September 16, we returned to survey twice more, on September 21 and October 6. Our highest count was on October 6, when we tallied 66 flowering stems. They ranged in height from about 12 cm to 36 cm tall. On our October 6 survey, most plants had at least some flowers still in bud towards the top of the stem, a few plants were completely in fruit, while a few others appeared to have recently emerged, with just the lower flowers beginning to open. We searched more areas of this field as well as other nearby sites that appeared to share similar habitat features and associated species, but we only found the *Spiranthes ovalis* var. *erostellata* within a single area encompassing approximately 0.2 hectare. Within this area, the plants tended to be clustered in three discrete groups of 18, 28, and 16 flowering stems, each group within an area of approximately 40–60 m^2. A few other plants were outliers, found singly.

The dominant associates in the meadow included locally common old field species such as *Danthonia spicata, Symphyotrichum pilosum* var. *pringlei*, and *Solidago juncea*. Other plant associates included such native species as *Carex pellita, Carex granularis, Euthamia graminifolia, Fragaria virginiana*, as well as non-native species including *Daucus carota, Euphrasia stricta, Agrostis gigantea*, and *Phragmites australis*. The wetter portions of the site, where *S. ovalis* var. *erostellata* was not found, included several interesting species, including a large (over 100 flowering stems) population of *Spiranthes magnicamporum*, which had been recently discovered in New York (Brunton 2015), as well as *Gentianopsis crinita, Solidago ptarmicoides, and Carex viridula.*

This species is easy to overlook. It is the latest-flowering *Spiranthes* species in northeastern North America and flowers at a time when not many botanists are in the field. Further it can easily hide in taller vegetation. While *S. magnicamporum* tends to stand out, *S. ovalis* var. *erostellata* can be missed. As the fill from the St. Lawrence Seaway construction is a relatively recent event, we wonder how long this species has been present at this site and how long will it remain? Will natural succession cause it to disappear?

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SYNOPSIS AND TYPIFICATION OF THE PASSIFLORACEAE NAMES IN RAFINESQUE'S PUBLICATIONS

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ABSTRACT

We discuss the names published and cited by Rafinesque between 1818 and 1838 that are relevant to the Passifloraceae sensu stricto and designate types and lectotypes when needed. An effort is made to preserve generic and infrageneric nomenclature through the choice of type species. The currently accepted names are given.

Passiflora L. (Linnaeus 1753: 955) with 600+ species (MacDougal & Feuillet, unpublished results) is the largest genus of the Passifloraceae s. str. Its species are mostly distributed in the New World with 14 species native in the continental USA (Goldman & MacDougal, 2015), including *P. incarnata* L., the type of the genus. Infrageneric categories have been described, split, and regrouped in various ways; new names and new combinations have been made by many authors; ex.: Jussieu (1789: 397–399); Rafinesque (1836: 102–104 [published mid-1838]); Bory (1819: 129–156); de Candolle (1822: 435–436; 1828: 321–337); Labillardière (1825: 78–79); Reichenbach (1828–1829: 132); Roemer (1846: 125–207); Karsten (1857: 438; 1860: 77, t. 38); Masters (1871: 625–639; 1872: 536–620); Triana & Planchon (1873: 126–180); Harms (1893: 86–92; 1925: 495–507); Cortés (1897: 73–74); Killip (1938: 24–76); Escobar (1988); Cervi (1997: 6–10); Feuillet & MacDougal (2003: 35–38); MacDougal & Feuillet (2004: 27–31). The current concept of a large genus *Passiflora* including *Tetrastylis* Barb. Rodr. (Barbosa Rodrigues 1882: 260), *Tetrapathea* Rchb. (Reichenbach 1828–1829: 132), and *Hollrungia* K. Schum. (Schumann 1887: 212) is supported by molecular data (Muschner et al. 2003; Yockteng & Nadot 2004; Krosnick & Freudenstein 2005; Hansen et al. 2006; Hearn 2006; Krosnick et al. 2013).

Because Rafinesque published in the first half of the 19th century and because he commonly redefined or replaced earlier names, including his own, with names he liked better, it is important to typify the generic and subgeneric names to stabilize their identity and when possible to avoid disturbing the currently accepted nomenclature. Rafinesque wrote prolifically on many disciplines: zoology, botany, geology, chemistry, mathematics, inventions, semiology, literature, meteorology, linguistics, anthropology ... in English, French, Italian, Latin ... (Warren 2004), but described taxa with a great economy of words and even letters as shown below. In his pamphlet titled Neogenyton,

Rafinesque (1825) described 66 new genera in four pages. Obviously, this style is detrimental to clarity.

Merrill (1949: 170–171) listed the 17 generic and infrageneric names published by Rafinesque (1818, 1819, 1836) in the Passifloraceae. Names are listed alphabetically, regardless of rank, with place of publication, status, species included. Merrill used only once the word 'type', much less than Rafinesque himself (1836).

RAFINESQUE'S SOMEWHAT CRYPTIC ABBREVIATIONS

Ad. = Michel Adanson (Adans.)

Andr. rep. = The botanist's repository vol. 5; text by John Kennedy 1802 (J. Kenn.); painting/engraving by Henry Charles Andrews (Andrews)

b. m. or b. mag. = Curtis's Botanical Magazine

Dec. = Augustin Pyrame de Candolle (DC.)

diff. = differs

do = ditto

G. = genus

J. or Jus. = Antoine Laurent de Jussieu (Juss.)

M. M. = American Monthly Magazine

N. [in 1818] = new

N [in 1819 & 1825] = Thomas Nuttall (Nutt.)

N [in 1836] = Noel Martin Joseph de Necker (Neck.)

N. G. = new genus

P. [in 1819] = Frederick Traugott Pursh (Pursh)

P. [in 1836] = Christiaan Hendrick Persoon (Pers.)

Pas. = *Passiflora*

R. = Constantin Samuel Rafinesque (Raf.)

Rheed. = Hendrik Adriaan van Rheede (Rheede), a pre-Linnean

Sm. = James Edward Smith (Sm.)

sq. = *squamis*

T. = Joseph Pitton de Tournefort (Tourn.), a pre-Linnean

tacs. = *Tacsonia*

W. = Carl Ludwig Willdenow (Willd.)

NOMENCLATURE

Rafinesque's names that belong in the Passifloraceae are presented in chronological order of publication, and for each date in alphabetical order. For each, the original text, usually very short, is cited in its entirety. In the quotes we follow the original fonts, except for the occasional characters in bold in the original that are not always very obvious. The types are cited or designated as well as the basionyms, and the currently accepted names are given.

A. 1815 Tableau de l'Univers

"PASSIFLOREA. Ex. G. Passiflora L. Murucuia Juss."

PASSIFLORACEAE Raf. (1815: 182, as "PASSIFLOREA"), later homonym.
= Passifloraceae Juss. (1805a) ex Roussel (1806: 334, as "Passifloreae"); nom. cons.

B. Baldwinia versus Balduinia 1818–1819

Rafinesque (Feb 1818: 267) wrote:

"*102. Passiflora peltata, must form the N.G. Baldwinia*"

without reference to the author or the publication of *Passiflora peltata* Cav. (1790: 447). Because there is no description and no reference to a previously published description, *Baldwinia* Raf. (1818) is invalid (McNeill et al. 2012: Art. 38.1) and *Balduina* Nutt. is a valid name in the Asteraceae.

Rafinesque later wrote (1819: 260):

"*49. Passiflora peltata, P., doit former un nouveau genre Balduinia, Raf. M. M., (janv.1818)*
50. Le genre Balduinia, N., doit donc être changé en Endorima, Raf. M. M., 1819"

It could be argued that, in comment 49, "P." for Pursh [1814: 445] associated with the orthographic variant is an indirect reference to a previously published description although Pursh cited Cavanilles (1790: t. 274) only as second (of three) reference after Willdenow (1800: 617 [Jan 1802]) who himself gave first his own description and then cited Cavanilles (1790: 447, t. 274), Tournefort (1700: 240), and Plumier (1693: 70, t. 85). Nevertheless, as noted in comment 50, *Balduina* Nutt., *nom. cons.*, (ASTERACEAE; Nuttall July 1818, 2: 175) is similar to *Baldwinia*. So *Balduinia* Raf. (1819), the most recent, is illegitimate (McNeill et al. 2012: Art. 60.Rec. 60B).

Baldwinia Raf. 1818: 267; invalid: no description.
Balduinia Raf. 1819: 260; orth. var.; illegitimate: later homonym of *Balduinia* Nutt. 1818.
Both based on *Passiflora peltata* Cav. 1790: 447, t. 274.
= **Passiflora** L. 1753

Index Kewensis (Jackson 1895) and IPNI (consulted 29 Sep 2017) cite *Baldwinia peltata*, but Rafinesque did not associate the two words in 1818 or 1819. Then in 1836 [1838] he placed *P. peltata* in *Meioperis* (see below). *Baldwinia peltata* Raf. ex Jackson, Index Kew. 1: 265. 1895; invalid: new combination in an invalid genus, with no intention to describe the genus.
Type: Based on *Passiflora peltata* Cav.
= **Passiflora suberosa** L. (1753: 958) subsp. **suberosa**.

Notes: In the Asteraceae, *Endorima* Raf. (1819: 260) is an illegitimate renaming of *Balduina* Nutt. (July 1818: 175) which is conserved against *Mnesiteon* Raf. (Oct–Dec 1817: 67).

C. 1836 Flora Telluriana [published mid-1838]

1. *Blephistelma* Raf. (1836: 103) [mid-1838]

"1128. BLEPHISTELMA R. (cil. crown) diff. Passifl. cal. tubuloso, petalis brevis, nect. tubul. lobato ciliato—Type: *Bl. aurantia* Raf. Murucuia do P. passifl. do Forst. W. Sm. Andr. rep. t. 295. fol. glabris 3-5lobis obt. New Caledon."

Blephistelma is a superfluous renaming of *Disemma* Labill. (1825: 78, t. 79); same type.
Type: *Blephistelma aurantia* Raf. (Rafinesque 1836: 103) [mid-1838]. = *Disemma aurantia* (G. Forst.) Labill. (1825: 78, t. 79). = **Passiflora aurantia** G. Forst. (Forster 1786: 62).
= **Passiflora** L. 1753

2. *Erndelia* Raf. (1836: 104) [mid-1838]

"1133. ERNDELIA Raf. non Necker, diff. Tacsonia cal. et cor. apex reflexa, corona duplice concentrica—Type *E. reflexiflora* Raf. Pas. do Cav. Tacs. do Pers."

Not *Erndelia* Neck. (Necker 1790 [see *Murucuia* below]; published in an opera utiq. oppr. See McNeill (2006), App. VI: 483. Not *Erndlia* Giseke (1792: 199, 209) ZINGIBERACEAE.

Type: *Erndelia reflexiflora* (Cav. 1799: 15, t. 425) Raf. = **Passiflora reflexiflora** Cav. 1799: 15, t. 425.
= **Passiflora** L. 1753

3. *Macrophora* Raf. (1836: 103) [mid-1838]

> "1125. MACROPHORA Raf. diff. Passifl. cal. tubo brevi, gynophoro longissimo, nect. dupl. series, stam. dilat. planis basi coactilis, antheris magnis—Type *M. sanguinea* Raf. Pass. do Sm. &c fol. 3lobis serratis acutis egland. cal. et ovar. toment. Antilles"

Type: *Macrophora sanguinea* (Sm.) Raf. 1836: 103 [mid-1838]. = *Passiflora sanguinea* Sm. (Smith 1814, 26(2): *Passiflora* N° 45). = **Passiflora quadriglandulosa** Rodschied (1794: 77).
= **Passiflora** L. 1753

4. *Meioperis* Raf. (1836: 103) [mid-1838].

> "1126. MEIOPERIS Raf. diff. Passifl. cal. 5part. petalis nullis, corona duplex, nect. sepe simplex planum—Types *M. peltata, suberosa, minima*[,] *pallida, multiflora, angustif.*[*olia,*] *pannosa, hederacea* &c, all Passifloras"

See under *Baldwinia* (above).
Lectotype here designated: *Meioperis peltata* (Cav. 1790: 447, t. 274) Raf. (1836: 103) [mid-1838].
= *Passiflora peltata* Cav. = **Passiflora suberosa** L. (1753: 958) subsp. **suberosa**.
= **Passiflora** L. 1753

Meioperis angustifolia (Sw.) Raf. 1836: 103 [mid-1838]. = *Passiflora angustifolia* Sw. (1788: 97). = **Passiflora suberosa** L. (1753: 958) subsp. **suberosa**.
Meioperis hederacea (Cav.) Raf. 1836: 103 [mid-1838]. = *Passiflora hederacea* Cav. (1790: 448). = **Passiflora suberosa** L. (1753: 958) subsp. **suberosa**.
Meioperis minima (L.) Raf. 1836: 103 [mid-1838]. = *Passiflora minima* L. (1753: 959). = **Passiflora pallida** L. (1753: 955).
Meioperis multiflora (L.) Raf. 1836: 103 [mid-1838]. = **Passiflora multiflora** L. (1753: 956).
Meioperis pallida (L. 1753: 955) Raf. 1836: 103 [mid-1838]. = **Passiflora pallida** L.
Meioperis pannosa (Sm.) Raf.(1836: 103) [mid-1838]. = *Passiflora pannosa* Sm. (1814: Passiflora no 28). = **Passiflora sexflora** Juss. 1805a: 110, t. 37:1.
Meioperis suberosa (L.) Raf. 1836: 103 [mid-1838]. = **Passiflora suberosa** L. (1753: 958).

5. *Modecca* Lam. 1797: 208

> "1124. MODECA Rheed. Jaq. diff Passifl. dioica, cal. tubul. 5fido. petalis 5, nect. sq. 5-10, stam. 5 liberis, ov. vix stipit. capsula 3valvis polysperma—Several Sp. 6 in Jaq. deviating by the free stamens and valvular capsule. Blended in India with the Convolv. called also Modeca, compare with the Euphorbides"

No species cited. "*Modeca* Rheed." orth. var. for *Modecca* Rheede 1688 (39–40, tab. 20).
Lectotype designated by Wilde (1971 (18): 20–23): *M. palmata* Lam. (1897; 4: 208). = **Adenia palmata** (Lam.) Engler (1891: 375).
= *Modecca* Lamarck 1797: 208 = **Adenia** Forsskål 1775: 77.

6. *Murucuia* [Tournefort 1694: vol. 1: 207; vol. 2: t. 125] Mill., Gard. Dict. Abr., ed. 4. 1754: vol. 2, pages not numbered.

"1127. MURUCUIA T. Jus. Pers. *Erndelia* Necker, diff. Passifl. cal. basi urceolatus, nect. tubuloso truncato—Type *M. ocellata* Pers. Pas. murucuia L. auct.—Persoon [1807: 222] had 3 sp. in this G. each being types of genera" [of Rafinesque; see *Blephistelma* above and *Peremis* below]

Type: *Murucuja lunata* Medik. (designated by Medicus 1787: 97). = **Passiflora murucuja** L. 1753: 957. *Murucuia ocellata* Pers. (1807: 222) has *Passiflora murucuja* in its synonymy. = **Passiflora** L. 1753

7. *Odostelma* Raf. (1836: 104) [mid-1838]

"1132. ODOSTELMA Raf. (toothed crown) diff. Tacsonia, corona dentata non glandulosa, stam. filam. planis—Types *O. pedunculata* and *adulterina* Raf. Tacsonia do auct."

Type: 2 syntypes. **Lectotype here designated**: *O. adulterina* (L. f.) Raf., Fl. Tellur. 4: 103. 1836. [mid-1838]. = **Passiflora adulterina** L.f. (1781: 408; published Apr 1782) = **Passiflora** L. 1753

Odostelma adulterina Raf., Fl. Tellur. 4: 104. 1836; [mid-1838] = **Passiflora adulterina** L. f. (1781: 408) [published Apr 1782]
Odostelma pedunculata Raf. 1836: 104 [mid-1838]. Probably an error for *P. peduncularis* Cav. If so = **Passiflora peduncularis** Cav. 1799: 15, t. 426.

8. *Passiflora* Raf. 1836: 102 [mid-1838]; "non L."

"1121. PASSIFLORA Raf. non L. This G. was badly understood by the Linneists, but reformed by Jussieu. Mine has *Perigono colorato basi urceol. limbo* 10*partito colorato*, 5 *alt. petaliformis. Corona multipartita. interna nectarif. basi urceol. gynophoro stam. 5 gerens basi connatis, stylis* 3, *fruct. bacca vel. pepo* (cysto Neck) *uniloc. polysp. placentas* 3, *sem. arillatis*—Many sp. in 3 subgenera—1 *Granadilla* Ad. no involucre—2 *Maracoa* Raf. fl. involucrate". [Rafinesque does not list a third subgenus; 3 might be a misprinting for 2]

Type: No species cited. Illegitimate: later homonym.
= **Passiflora** L. 1753

8a. Subg. *Granadilla* (Adans. 1763: 408) **Raf. 1836: 102 [mid-1838].**

[Passiflora subg.] "1 *Granadilla* Ad. no involucre"

No species cited. The basionym *Granadilla* Mill. (1754: alphabetical treatment, no page numbers) includes the type of *Passiflora* L. in its non-binominal form. In Adanson (1763: 563), the author cited by Rafinesque, *Granadilla* Monardes (1580: pages not numbered) includes *Passiflora* L. = **Passiflora** L. subg. **Passiflora**

Notes: The use and text of *Granadilla* by Monardes must date from 1574, but we have seen only the 1580 reprint reputed unchanged of the 1565, 1569 and 1574 parts of his Historia medicinal: de las cosas que se traen de nuestras Indias Occidentales, que sirven en Medicina. In the reprint, *Granadilla* is in part 3 (sheet 89 of the whole reprint).

Passiflora subg. *Granadilla* (P. Miller) Rchb. Consp. 132 (Dec 1828–Mar 1829) should be **Passiflora** L. subg. **Passiflora**.

The lectotypification of *Passiflora* subg. *Granadilla* (Medic.) Mast. (Trans. Linn. Soc. 27: 635. 1871) is superfluous. = **Passiflora** L. subg. **Passiflora**

Granadilla P. Miller, Gard. Dict. Abr. ed. 4 (unpaged). 28 Jan 1754. [*Granadilla* was made superfluous (but not illegitimate) by the latter choice of *Passiflora incarnata* L. 1753 as the lectotype of *Passiflora* L. (Killip 1938: 24; cf. Jarvis et al. 1992: 567). As a subgenus of *Passiflora*, *Granadilla* was lectotypified by Killip (1938) who selected *Passiflora caerulea* L. 1753. At the same time Killip placed *Passiflora incarnata* in subgenus *Granadilla*, and accepted it as the lectotype of the genus. According to the "Code" (McNeill et al. 2012, ICBN, art. 22.1), this subgenus should be called *Passiflora* subg. *Passiflora* and have *Passiflora incarnata* for type.
    = **Passiflora** L. 1753.

Passiflora subg. *Granadilla* (Mill.) Rchb. (1828–1829) is a superfluous combination, as well and its lectotypification by Killip (1938: 30; *P. caerulea* L.) is invalid as the subgenus includes the type of *Passiflora* (*P. incarnata* L.). Subgenus *Granadilla* was used well into the 20ᵗʰ century and accredited to various authors like (Medik.) Mast. by Killip (1938: 29).

8b. Subg. *Maracoa* Raf., Flora Tellur. 4: 102. 1836. [mid-1838]

[Passiflora subg.] "2 *Maracoa* Raf. fl. involucrate"

Type: no species listed. Type **here designated**: *Passiflora incarnata* L. 1753: 959.
= **Passiflora** L. subg. **Passiflora**

Notes: *Maracoa* is undoubtedly derived from maracoc or maracock, one of the vernacular names of *Passiflora incarnata* (type of *Passiflora* L.) reported from Virginia in the XVIIe century by Captain John Smith. There is no indication in the protologue of the species it may include, and the text, "Fl. involucrate", could match most species of *Passiflora* subg. *Passiflora*.

Captain John Smith, President of Virginia (for a couple of months) and perhaps most famous for his relationship with Pocahontas, noted in his diary the common Algonquian name of "Maracock" for a cultivated plant, most surely *Passiflora incarnata*. It is mentioned and illustrated by Parkinson (1629: 393–396) as "Jesuites Maracoc" (see also Endersby 2007: 31; Kugler 1995; and Kugler and King 2004). The similarity of the words *maracock, maracoa, mbaracuja, murucuja,* and *murucuia,* all vulgar names used for centuries in Virginia and the West Indies and Brazil for kinds of passionflowers, is surely not a coincidence, but we have not seen a satisfactory explanation of its real origin.

9. *Peremis* Raf., Fl. Tellur. 4: 104. 1836. [mid-1838]

"1129. PEREMIS Raf. (around half) diff. Passifl. no petals, calix globular—Type *P. orbiculata* R. Murucuia P. Passifl. Cav."

Type: *Peremis orbiculata* (Cav. Diss. 10, Decima Diss. Bot. 456) Raf. 1836: 104.
Peremis orbiculata (Cav.) Raf., Fl. Tellur. 4: 104. 1836. [mid-1838]. = **Passiflora orbiculata** Cav. (1790: 456).
= **Passiflora** L. 1753

10. *Pericodia* Raf., Fl. Tellur. 4: 104. 1836. [mid-1838]

> "1134. PERICODIA R. diff. Pass. fl. cal. campanul. lac. subul. petalis dilat. nect. plicato— Type P. *perfoliata* Raf. Passifl. do L."

Type: *Pericodia perfoliata* (L.) Raf. 1836: 104.
Pericodia perfoliata (L.) Raf., Fl. Tellur. 4: 104. 1836 [mid-1838]. = **Passiflora perfoliata** L. (1753: 956).
= **Passiflora** L. 1753

11. *Synactila* Raf., Fl. Tellur. 4: 104. 1836. [mid-1838]

> "1130. SYNACTILA Raf. (un. rays) diff. Passi . no petals, rays of nectary united at the base in a cyl. crown inserted on the tubular 5parted calyx.—Type *S. viridiflora* R. Pass do Cav. W."

Type: *Synactila viridiflora* (Cav.) Raf.
Synactila viridiflora (Cav.) Raf., Fl. Tellur. 4: 104. 1836. [mid-1838]. = **Passiflora viridiflora** Cav. (1799: 15, t. 424)
= **Passiflora** L. 1753

12. *Tacsonia* Juss. 1789: 398

> "1131. TACSONIA Juss. diff. Passifl. cal. tubul. 10fidus, coloratus, corona glandulis, gynophoro elongato—Many sp. in 4 subgenera."

12a. *Tacsonia* subg. *Balostis* Raf., Flora Tell. 4: 104. 1836. [mid-1838]

> [*Tacsonia* subgen.] "4. *Balostis* R. Cal. globoso, type P. glauca auct. is it a Genus? how is the crown?"

The description, "cal. globoso", does not match the funnel-shaped floral tube of *P. glauca* Bonpland (1808: 76, t. 22), but it fits slightly better the campanulate hypanthium of *Passiflora glauca* Aiton (1789: 308).

Lectotype (designated by Merrill 1949: 170): *Passiflora glauca* Aiton (= **P. stipulata** Aubl. 1775: 830, t. 325).
= **Passiflora** subg. **Passiflora**

12b. *Tacsonia* subg. *Perimna* Raf., Flora Tell. 4: 104. 1836 [mid-1838]

> [*Tacsonia* subgen.] "1. *Perimna* Raf. invol. nullis"

Rafinesque did not cite any species. A species, published in a work cited by Rafinesque (1836), that has three inconspicuous small bracts inserted at different levels is chosen as the type.

Type here designated: *Tacsonia glandulosa* (Cav.) Juss. 1805b: 391. = **Passiflora glandulosa** Cav. 1790: 453, t. 281.
= **Passiflora** subg. **Passiflora**

12c. *Tacsonia* Juss. subg. *Siphostegia* Rafinesque 1836: 104 [mid-1838]

[*Tacsonia* subgen.] "3. *Siphostegia* Raf. invol. tubuloso"

Rafinesque did not cite any species. A species well known at the time and having the bracts partly fused in a tubular structure is *Tacsonia mixta* (L.f.) Juss. (1805b: 394).

Lectotype here designated: *Tacsonia mixta* (L.f.) Juss. = **Passiflora mixta** L. f. 1781: 408 [Jan 1782].
= **Passiflora** subg. **Passiflora**

12d. *Tacsonia* Juss. subg. *Tristegia* Rafinesque 1836: 104 [mid-1838]

[Tacsonia subgen.] "2 *Tristegia* Raf. invol. 3phylo"

Rafinesque did not cite any species. A species that has three small bracts, published in a work cited by Rafinesque (1836), is chosen as the type. It has 3 bracts free and involucrate.
Type here designated: *Tacsonia pinnatistipula* (Cav.) Juss. 1805b: 393. = **Passiflora pinnatistipula** Cav. (1799: 428)
= **Passiflora** subg. **Passiflora**

13. *Tripsilina* Raf. 1836: 103 [mid-1838]

"1122. TRIPSILINA Raf. diff. Passiflora, fl. involucratis bipinnatif. petalis cal. eq. nect. filif. brevis, capsula inflata, placentas 3 internis seminiferis—Type *Tr. fetida* R. Pas. do L. b. m. 2619, seen alive. All the capsular sp. must be divided of course from the baccate kinds."

Type: *Tripsilina foetida* (L.) Rafinesque 1836: 103 [mid-1838] "as "*fetida*". = **Passiflora foetida** L. 1753: 959.
= **Passiflora** L. 1753

Note: Passiflora foetida fruits are not capsular, but the berries are indeed inflated and have a thin somewhat dry pericarp, unlike most of the other "baccate kinds".

14. *Xerogona* Raf. (1836: 103) [mid-1838].

"1123. XEROGONA Raf. diff. Passifl. petalis brevior, corona brevi, nect. int. duplice cupula. 6gona plac. 3 int. seminif.—Type *X. biloba* Raf. Pas. capsularis L. auct. Dec. b. mag. 2868. 3 var. fol. bilobis, fol. bifidis, fol. maculatis."

Notes: *Xerogona biloba* Raf. (1836: 103) [mid-1838]. There are several ways the type citation could be interpreted. One way is as two syntypes, recognizing both *X. biloba* and *P. capsularis* in which case *X. biloba* is a nomen nudum. We think this not likely and in two other cases in this same publication, Rafinesque used the plural "Types" when more than one species was cited (see above, *Meioperis* and *Odostelma*). Second, it could be interpreted that *X. biloba* was presented as a name for *P. capsularis* auct., non L., but the two cited references of description by de Candolle (1828: 325) and WJ Hooker (1828: pl. 2868) are clearly *P. capsularis* L. with minor variations in leaf shape and maculation. The third interpretation is that Rafinesque was bringing together under one name, *X. biloba*, the known variants of the species and recognizing them as three unnamed varieties. This view we think is most likely, but the Linnean epithet should have been retained, and we interpret the name *X. biloba* as an illegitimate renaming of the previously published *P. capsularis* L. As we know well the identity of *Passiflora capsularis* L., this is the obvious choice for a type.

Lectotype here designated: **Passiflora capsularis** L. (1753: 957)
= **Passiflora** L. 1753

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HIRTELLA CRUSA (CHRYSOBALANACEAE), UNA ESPECIE NUEVA DE LA PENÍNSULA DE OSA, COSTA RICA

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RESUMEN

Se describe e ilustra **Hirtella crusa** Aguilar & D. Santam. (Chrysobalanaceae), una nueva especie de la Península de Osa, Provincia de Puntarenas, Costa Rica. Esta especie es un árbol pequeño, con láminas foliares angostas e inflorescencias paniculadas, con las glándulas de las bractéolas sésiles y conspicuamente verrucosas. Se considera en este trabajo que el nombre más apropiado para material costarricense identificado como *Hirtella davisii*, recientemente reportada para el país, sea *H. excelsa*. También se brinda una clave para las 11 especies costarricenses de *Hirtella,* y se ilustra con fotos a color nueve de ellas.

ABSTRACT

A new species, **Hirtella crusa** Aguilar & D. Santam. (Chrysobalanaceae), is described and illustrated from the Osa Peninsula, Puntarenas Province, Costa Rica. This species is a small tree with narrow, almost glabrous leaves and paniculate inflorescences, with the marginal bracteolar glands sessile and conspicuously-verrucose. We consider that the most appropriate name to use for Costa Rican material identified as *Hirtella davisii*, recently reported from the country, is *H. excelsa*. Also, we provide a key to the 11 Costa Rican species of *Hirtella*, nine of which are illustrated with color photos.

Hirtella L. comprende 105 especies en los Trópicos y Subtrópicos de América, y dos especies en África y Madagascar, y es el segundo género con mayor número de especies en la familia Chrysobalanaceae (Malpighiales), luego de *Licania* Aubl. sensu lato (ca. 214 especies). El género se reconoce morfológicamente por sus flores con 3–9 estambres exsertos, organizados unilateralmente y casi separados hasta la base, y el receptáculo hueco, con el ovario unilocular e inserto en la boca; además, sus inflorescencias tienen bractéolas que usualmente son glandulares (Prance & Sothers 2003; Sothers et al. 2016; Camargo Asprino & Amorim 2016; Asprino & Amorim 2016).

En Costa Rica, el género cuenta con 11 especies y dos variedades; siete de ellas se encuentran en la Península de Osa, incluida una variedad y la nueva especie aquí descrita (Prance, inéd.; Aguilar et al., 2017). Las especies de *Hirtella* en Costa Rica se encuentran distribuidas en diversos ecosistemas, tales como bosque seco y bosque muy húmedo sobre ambas vertientes, entre los 0–1700 metros de elevación. *Hirtella racemosa* var. *hexandra* (Willd. ex Roem. & Schult.) Prance y *H. triandra* Sw. son las especies más comúnmente recolectadas y con más amplia distribución en el país, mientras que otros taxones, como *H. papillata* Prance, *H. racemosa* Lam. var. *racemosa*, y *H. trichotoma* Prance, son conocidos de pocas recolecciones y con distribución restringida a ciertas

regiones de Costa Rica; también, de la última, luego de su publicación (Prance 1992) a la actualidad, todavía se desconocen sus frutos.

Las exploraciones sistemáticas en la Península de Osa, han revelado un número importante de novedades taxonómicas, como nuevas especies (p.ej., Hammel 2015; Linares 2015; Morales & Zamora 2017; Santamaría-Aguilar & Lagomarsino 2017; Santamaría-Aguilar et al. 2017), nuevos registros para la flora de Costa Rica (p.ej., *Justicia secunda* Vahl, Acanthaceae; *Lathrophytum peckoltii* Eichler, Balanophoraceae; *Slonea paucinervia* T.D. Penn., Elaeocarpaceae), o especies que por primera vez son encontrados en la Península, aunque conocidas de otros lugares en Costa Rica (p.ej., *Chamguava schippii* (Standl.) Landrum, Myrtaceae; *Gibsoniothamnus epiphyticus* (Standl.) L.O. Williams, Schlegeliaceae; *Solanum campechiense* L., Solanaceae). De esta manera, en la siguiente contribución describimos una nueva especie de *Hirtella*, endémica por el momento a la zona anteriormente mencionada, la cual es prioridad para su conservación por la destrucción actual de su hábitat para el cultivo de palma para extraer aceite (*Elaeis* sp., Arecaceae) (Fig. 1, J–K). Aunque el segundo autor ha realizado una intensa búsqueda por más de tres años en las cercanías de la localidad tipo con el fin de ubicar más individuos, no se tuvieron resultados esperados. Por lo cual con el material disponible es descrita a continuación, y que la descripción de esta nueva especie constituye el primer paso para que se tomen las medidas para su conservación.

HIRTELLA CRUSA Aguilar & D. Santam., **sp. nov.** TIPO: **Costa Rica. Puntarenas.** Reserva Forestal Golfo Dulce, Rincón, cuenca oeste de la quebrada Aguabuena, 8°42'00"N, 83°30'55"W, 0 m, 26 Mar 2012 (fl.), *D. Santamaría-Aguilar & R. Aguilar 9371* (holotipo: MO-6673478!; isotipos: CR-n.v., GH!). Figura 1A–I.

Hirtella crusa is morphologically similar to *H. piresii* Prance from South America, with which it shares linear stipules, narrow, almost glabrous leaves, acuminate at the apex, axillary, paniculate inflorescences, with the rachis scarcely pubescent and the bracts and bracteoles with sessile glands, and flowers with three stamens. *Hirtella crusa* differs by its semiorbicular and conspicuously glandular-verrucose bracteoles, with the glands sometimes extending beyond the margin (vs. oblong to lanceolate or triangular bracteoles, with a single reflexed apical gland).

Arbolito de 10 (–20) m de altura. Ramitas jóvenes glabras a esparcidamente pubescentes, los tricomas ca. 1 mm de longitud, amarillentos. Hojas con estípulas de 0.3–0.4 cm de longitud, lineares, esparcidamente pubescentes, eglandulares, tardíamente decíduas; pecíolo de 0.1–0.2 cm de longitud, terete, eglandular, esparcidamente pubescente, los tricomas pardo claro a amarillentos; lámina de 8.8–9.2 × 2.2–2.5 cm, oblongo-lanceolada, secando pardo claro a verde oliva; base atenuada a subcuneada; ápice acuminado; haz glabro, no bullado; envés glabro y con papilas blanquecinas, además con glándulas aplanadas dispersas por la superficie, no bullado; vena media levemente elevada en ambas caras, papilosa en el haz, muy esparcidamente pubescente en el envés; venas laterales 10–12 por lado, planas y glabras en la haz, levemente elevadas y muy esparcidamente pubescentes en el envés, las venas terciarias apenas visibles en ambas caras. Inflorescencias axilares, especialmente saliendo hacia el ápice de las ramas, paniculadas, de 6.5–9 cm de longitud, erectas, el raquis terete a levemente aplanado, muy esparcidamente pubescente, los tricomas pardo claro a amarillentos, de 0.5–1 mm de longitud; bráctea 1, de 2.5–3 mm de longitud, angostamente triangular, delgada, posiblemente caduca, la cara externa con tricomas similares a los del raquis, la cara interna usualmente glabra, el margen con 1 o 2 glándulas sésiles por lado; bractéolas opuestas, de 1–2 × 0.8–1.5 mm, semiorbiculares, gruesas, persistentes, glabras o con escasos y dispersos tricomas en ambas caras, algunas veces la parte central por la cara interna con el indumento más denso, el margen conspicuamente glanduloso-verrucoso, las glándulas sésiles, algunas veces más allá del margen. Flores con el pedicelo 4–6 mm de longitud, sin glándulas, glabro; receptáculo de 1–1.5 mm de longitud, campanulado, engrosado en uno de los lados, glabro por afuera, glabro por dentro, excepto densamente pubescente en la garganta; cáliz con (4) 5 lóbulos ca. 2.5 × 1.5–2 mm, oblongos, reflexos

luego de la antesis, glabros en ambas caras, pero con tricomas en el ápice sobre ambas caras, los tricomas amarillentos, el margen eglandular, algunas veces con tricomas; pétalos (4) 5, 3–4.5 × 2–2.5 mm, blancos, glabros sobre ambas caras; estambres 3, unilaterales, de 13–15 mm de longitud, blancos en la base y morado-purpura distalmente, glabros, con 1 o 2 estaminodios filamentosos opuestos a los estambres, de 1.5–2 mm de longitud, glabros; ovario inserto en el ápice del receptáculo, ca. 1 × 1 mm, pubescente (especialmente hacia el ápice), lateralmente aplanado, el ápice con 2 o 3 pequeños lóbulos; estilo ginobásico, de 12–16 mm de longitud, morado-purpura, filiforme, densamente pubescente en la base, los tricomas amarillentos a pardo claro. **Frutos** desconocidos.

Hábitat y distribución. *Hirtella crusa* es endémica de Costa Rica, donde en apariencia parece estar restringida a la Península de Osa, en las cercanías de la comunidad de Agua Buena de Rincón (Fig. 2). Crece en las partes bajas de las serranías, junto a las quebradas y sobre terreno undulado.

Fenología. Flores han sido recolectadas en marzo.

Etimología. El epíteto específico, *crusa,* es nombrado en honor para la Fundación Costa Rica-Estados Unidos para la Cooperación (CRUSA), por su apoyo a la conservación de la biodiversidad de la Península de Osa y al desarrollo humano de sus habitantes.

Hirtella crusa se reconoce por sus estípulas lineares, láminas foliares angostas, casi glabras y papilosas en el envés y con glándulas aplanadas en diferentes partes; inflorescencias paniculadas, con el raquis muy esparcidamente pubescente y las brácteas y bractéolas con glándulas sésiles en los márgenes, las de las bractéolas conspicuamente glandular-verrucosas; y flores con el receptáculo campanulado, los lóbulos del cáliz eglandulares, con pubescencia en el ápice en ambas caras, y tres estambres.

Otras características adicionales a las presentadas en la diagnosis para diferenciar *Hirtella crusa* de *H. piresii* son las estípulas más cortas (0.3–0.4 cm vs. 0.1 cm de longitud), las láminas foliares con las venas terciarias apenas visibles (vs. fuertemente impresas en ambas caras), inflorescencias con las brácteas más cortas (2.5–3 mm vs. 5–8 mm de longitud), las bractéolas opuestas (vs. alternas), y las flores con pedicelos de 4–6 mm de longitud (1.5–3 mm).

Siguiendo la clave publicada por Prance & Sothers (2003), *Hirtella crusa* queda cerca de los taxones suramericanos *H. bahiensis* Prance y *H. davisii* Sandwith, por tener inflorescencias paniculadas, con bractéolas con numerosas glándulas en el margen. Sin embargo, en *H. bahiensis* y *H. davisii* las glándulas de las bractéolas son estipitadas (vs. bractéolas con glándulas sésiles). Mientras que las láminas foliares *H. bahiensis* son pequeñas (1.8–4.5 cm longitud) y en *H. davisii* tienden hacer más grandes (6–13.5 cm de longitud) (vs. 8.8–9.2 cm de longitud en *H. crusa*).

En Costa Rica, se conocen las siguientes seis especies de *Hirtella* con inflorescencias paniculadas y tres estambres*: H. americana* L., *H. guatemalensis* Standl., *H. papillata* Prance, *H. triandra* Sw. y *H. trichotoma* Prance, todas con láminas foliares en el envés y ejes de la inflorescencia pubescentes (vs. láminas foliares casi glabras en el envés y ejes de la inflorescencia muy esparcidamente pubescentes en *H. crusa*); y *H. media* Standl., como tratada por Zamora (2000) y Zamora et al. (2004), de la vertiente Caribe en las Provincias de Guanacaste, Heredia y Limón. Con esta última, además de las características de las inflorescencias y cantidad de estambres, *H. crusa* también comparte las láminas foliares casi glabras en el envés; sin embargo, *H. media* difiere por la inflorescencia con el raquis densamente pubescente, con bractéolas eglandulares, y los lóbulos del cáliz densamente pubescentes (vs. inflorescencia con el raquis muy esparcidamente pubescente, con bractéolas glandulares, y lóbulos del cáliz glabros). Adicionalmente, las láminas foliares de *H. media* usualmente son más pequeñas (5.1–7.1 × 2.1–2.5 cm, vs. 8.8–9.2 × 2.2–2.5 cm). En Costa Rica, y a razón de sus láminas foliares casi glabras en el envés, la nueva especie se podría confundir con *H. excelsa,* pero se puede diferenciar por la característica mencionada en clave (copla 1 y 3).

Especimen adicional examinado. COSTA RICA. Puntarenas. [Cantón de Osa] Baneguitas, 3 km WSW of Rincón, 1 km S of Vidal's pulpería in Aguabuena, in pasture of Mariano from Cangreja, 8°41' N, 83°31' W, 30 m, 14 Mar 1993 (est.), *Thomsen 266* (CR).
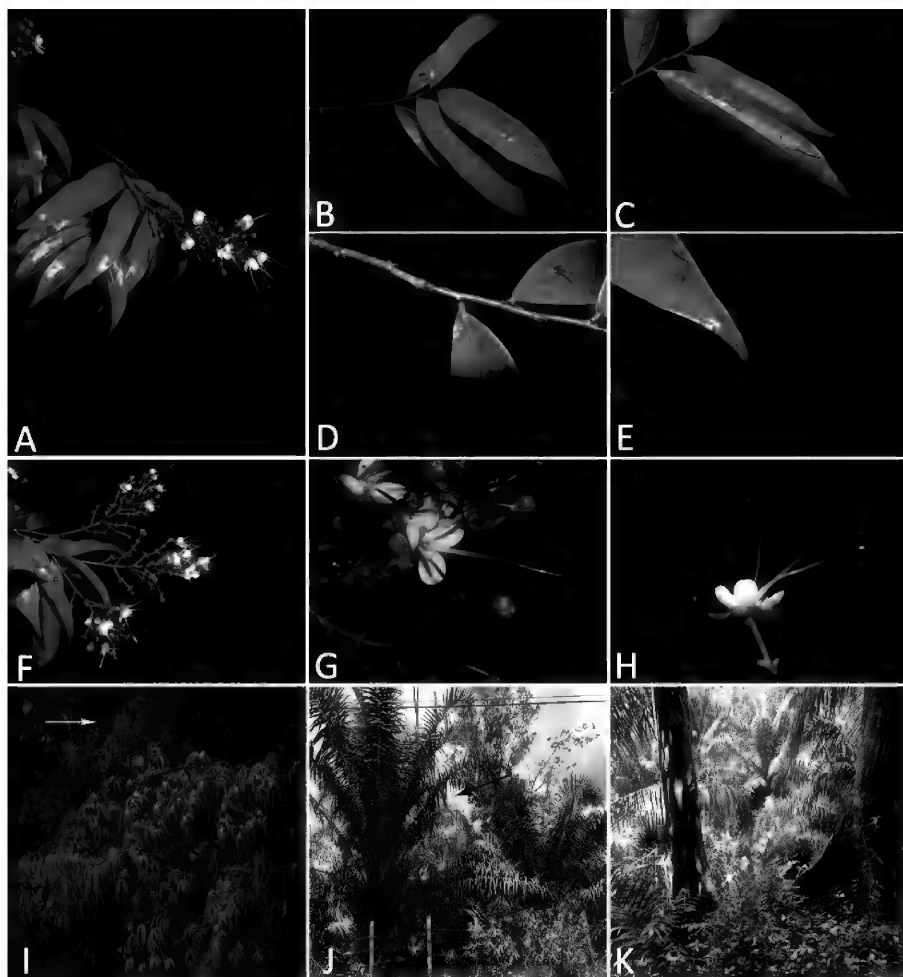
Figura 1. *Hirtella crusa.* **A.** Rama con inflorescencias. **B.** Haz de las láminas foliares. **C.** Envés de las láminas foliares. **D.** Base de las láminas foliares. **E.** Ápice de la lámina foliar. **F.** Inflorescencias. **G.** Flores. **H.** Flor con dos bractéolas. **I.** Rama con hojas (flecha) y lugar donde se encontraba la especie, los frutos anaranjados corresponden a *Brosimum lactescens* (S. Moore) C.C. Berg (Moraceae). **J, K.** Uso actual de la tierra, la flecha mostrando el lugar aproximado donde ocurría la nueva especie y anillado de los árboles. Fotografías por R. Aguilar, A–H de *Santamaría & Aguilar 9371.*
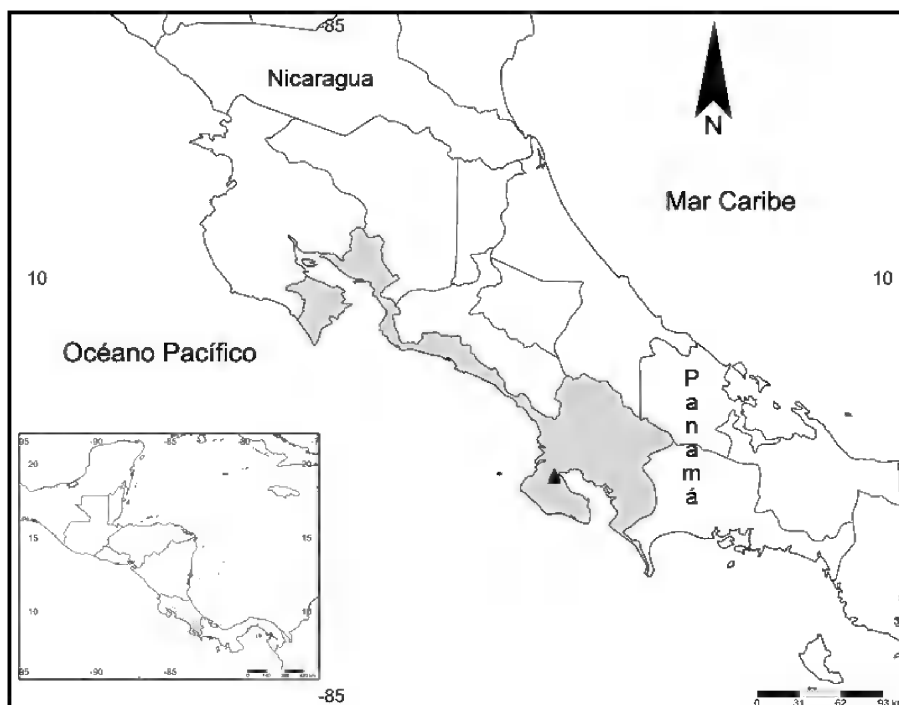
Figura 2. Distribución de *Hirtella crusa* (▲), con la Provincia de Puntarenas sombreada.

CLAVE PARA LOS TAXONES COSTARRICENSES DE *HIRTELLA*
(*Especies conocidas de la Península de Osa)

1. Inflorescencia un racimo.

    2. Flores con 3 estambres.

        3. Láminas foliares en el envés y ejes de la inflorescencias muy esparcidamente pubescentes; margen de los lóbulos del cáliz glandulares; pedicelos eglandulares; bractéolas con numerosas glándulas marginales .... ***H. excelsa**

        3. Láminas foliares en el envés y ejes de la inflorescencias densamente pubescentes; margen de los lóbulos del cáliz eglandulares; pedicelos eglandulares o con 1–4 glándulas; bractéolas solamente con una glándula apical .... ***H. lemsii** (Fig. 3C–I)

    2. Flores con 5–7 estambres.

        4. Bractéolas con glándulas marginales sésiles, o con una glándula apical; fls. con el pedicelo de (3–) 5–10 mm de longitud; receptáculo campanulado; lóbulos del cáliz reflexos y sin glándulas en el margen .... **H. racemosa**

           4a. Láminas foliares 3.5–10.2 cm de longitud, redondeadas a cuneadas en la base; bractéolas con las glándulas marginales pequeñas, planas, o sólo con una glándula apical; pedicelos delgados .... ***H. r. var. hexandra** (Fig. 3N–O)

4b. Láminas foliares (7–) 11–16 cm de longitud, generalmente subcordadas en la base; bractéolas mayormente con glándulas marginales grandes, cóncavas; pedicelos generalmente gruesos .... **H. r. var. racemosa** (Fig. 3P–Q)

4. Bractéolas eglandulares; fls. con el pedicelo de 0.5–1 (–1.5) mm de longitud; receptáculo tubular; lóbulos del cáliz erectos y con inconspicuas glándulas en el margen ....***H. tubiflora** (Fig. 3U–W)

1. Inflorescencia una panícula.

5. Brácteas y bractéolas (usualmente) eglandulares.

6. Láminas foliares 5–7.4 × 2.1–3 cm, la vena media y las venas laterales glabrescentes en el envés; inflorescencias con los ejes tomentosas, brácteas y bractéolas 1.5–2.5 mm de longitud; frutos maduros esparcidamente pubescentes .... **H. media** (Fig. 3J)

6. Láminas foliares 8.7–15 × 3.9–5.2 cm, la vena media y las venas laterales hirsútulas en el envés; inflorescencias con los ejes hirsútulos, brácteas y bractéolas (2.5–) 3–5 mm de longitud; frutos maduros densamente pubescentes .... ***H. triandra** (Fig. 3R–T)

5. Brácteas y bractéolas glandulares.

7. Bractéolas con glándulas estipitadas.

8. Bractéolas con glándulas marginales muy conspicuas (no muy distintivas en inflorescencias poco desarrolladas); frutos 1.4–7 × 0.8–1.1 cm, esparcidamente pubescentes; ramitas, láminas foliares por el envés y ejes de la inflorescencias densamente tomentosas **H. americana** (Fig. 3A)

8. Bractéolas con glándulas marginales inconspicuas, o con una glándula apical; frutos 3.5–4.4 × 2–2.7 cm, densamente pubescentes; ramitas, láminas foliares por el envés (especialmente sobre la vena media) y ejes de la inflorescencias esparcidamente híspidas a hirsutas .... **H. guatemalensis** (Fig. 3B)

7. Bractéolas con glándulas sésiles.

9. Láminas foliares 2.2–2.5 cm de ancho, la base base atenuada a subcuneada; ejes de la inflorescencias muy esparcidamente pubescentes .... ***H. crusa** (Fig. 1A–I)

9. Láminas foliares 5.6–9.5 cm de ancho, la base obtusa a subcordada; ejes de la inflorescencias densamente pubescentes.

10. Ramitas y envés de las láminas foliares con tricomas no notables al tacto y la vista; ejes de la inflorescencia densamente tomentosos; brácteas triangulares; vertiente Pacífica .... ***H. papillata** (Fig. 3K–M)

10. Ramitas y envés de las láminas foliares con tricomas notables al tacto y la vista; ejes de la inflorescencia hirsutos; brácteas lineares; vertiente Caribe .... **H. trichotoma**

Notas misceláneas sobre *Hirtella* de Costa Rica

Hirtella davisii, con inflorescencias paniculadas, bractéolas con numerosas glándulas estipitadas (0.3–1 mm de longitud), y los márgenes de los sépalos eglandulares; recientemente ha sido reportada para Costa Rica, por una muestra con frutos recolectada en la Península de Osa (*Aguilar 1183*, CR-3 cartulinas, MO). También ha sido reportada de Nicaragua, y disyuntamente en Venezuela, Guyana (de donde el tipo), Guyana Francesa y Brasil (Prance, 2001; Prance & Sothers, 2003; Prance, inéd.). Sin embargo, tras estudiar el material de Costa Rica y Nicaragua (*Luna 270*, MO [fl.]; *Moreno 25541*, MO-2 cartulinas [fl.]; *Moreno 25614*, MO [fl.]), hemos observado que todas esas recolecciones tienen inflorescencias racemosas, con los márgenes de las brácteas y bractéolas, así como los de los sépalos, con glándulas sésiles o subsésiles en el margen (ca. 0.1 mm de longitud). Con base en las características antes mencionadas, consideramos que el mejor nombre para aplicar a esas recolecciones es *H. excelsa* Standl. ex Prance, también distribuida en Ecuador, Perú, Bolivia y Brasil.

Figura 3. Especies de *Hirtella* en Costa Rica. **A.** *Hirtella americana*, flores, fruto maduro (en recuadro) y glándulas. **B.** *H. guatemalensis*, fruto y envés de la lámina foliar. **C–F.** *H. lemsii*, haz de las láminas foliares (C), ramita mostrando el indumento y bases de las láminas foliares (D), inflorescencia, flecha señalando la glándula (E), fruto (F). **G–I.** *H. lemsii* (vertiente del Caribe), rama con hojas e inflorescencias (G), flores, la flecha señalando el pedicelo eglandular (H), frutos (I). **J.** *H. media*, envés de las láminas foliares. **K–M.** *H. papillata*, rama con hojas e inflorescencias (K), flores (L), frutos (M). **N, O.** *H. racemosa* var. *hexandra*, rama con hojas (N), inflorescencias (O). **P, Q.** *H. racemosa* var. *racemosa*, envés de las láminas foliares (P), flores (Q). **R–T.** *H. triandra*, rama con hojas e inflorescencias (R), flores (S), fruto (T). **U–W.** *H. tubiflora*, rama con hojas e inflorescencias (U), botones florales y flores (V), frutos (W). Fotografías por O.M. Montiel (A), de *Stevens 29931*; I. Coronado (B), de *Coronado 4708*; E. Salicetti (G, H); R. Moran (I); O. Vargas (J); N. Zamora (P, Q); L. Martínez (U–W), de *Martínez 1742*; y R. Aguilar (C–F, K–M, N–T), de *Aguilar 11392* (C, D, F), *Santamaría & Aguilar 9860* (E), *Santamaría et al. 9849* (K–M) y *Santamaría & Aguilar 9861* (R–T).

La recolección *Nelson & Cruz 9493* (MO), del Departamento de Gracias a Dios, Honduras y en condición estéril (al menos el duplicado en MO), es mencionada por Prance (inéd.) bajo *Hirtella lemsii*, pero es un poco dudosa que sea dicha identidad.   Esa recolección más bien podría corresponder a *H. guatemalensis*, ya que tiene láminas foliares oblongas, con la base redondeada a subcordada, el envés con pocos tricomas y los peciolos que se tornan glabros con la edad, además es un taxón conocido de esa región; ver, por ejemplo, *House s.n.* (MO), *House & Cubas 2816* (MO), y Zamora (2000). *Hirtella lemsii*, como aquí interpretada, es conocida del Pacífico Sur de Costa Rica y de la vertiente Caribe en Nicaragua (Departamento Río San Juan, Reserva Indio Maíz) y Costa Rica (Heredia, principalmente en la Estación Biológica La Selva).   Aunque las recolecciones de ambas vertientes comparten pubescencia híspida (usualmente), láminas foliares similares en tamaño y con la base subcordada, inflorescencias racemosas y flores con tres estambres, el material de la vertiente Caribe (Fig. 3G–I), difiere por sus brácteas y pedicelos usualmente eglandulares (vs. siempre con glándulas) y estambres siempre más cortos (6–9 mm vs. 13–15 mm de longitud), además de la disyunción geográfica (Caribe vs. Pacífico).

AGRADECIMIENTOS

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SOLIDAGO SPELLENBERGII (ASTERACEAE: ASTEREAE), A NEW SPECIES OF GOLDENROD FROM MEXICO

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ABSTRACT

A new species of goldenrod, **Solidago spellenbergii** Semple, is described from a collection from Chihuahua, Mexico. The species was originally identified as *S. wrightii*, but the specimen does not fit well into that species. The holotype was included in a multivariate analysis of *Solidago* subsect. *Thyrsiflorae* and was placed a posteriori into a position between *S. petiolaris*, *S. orientalis*, and *S. buckleyi* with low probabilities to these species and with even less probabilities into *S. capulinensis* and *S. wrightii*. The species is distinguished from *S. wrightii*, the likely closest relative, on the basis of leaf and ovary/fruit traits. The species is named in honor of one of its collectors, Richard W. Spellenberg.

Solidago subsect. *Thyrsifloriae* includes *S. buckleyi* Torr. & A. Gray, *S. capulinensis* Cockerell & Andrews, *S. correllii* Semple, *S. orientalis* (Nesom) Nesom, *S. petiolaris* Ait., and *S. wrightii* A. Gray (Nesom 1989, 1990, 2008; Semple & Cook 2006; Nesom & Lowrey 2011; Semple 2017; Semple 2017 frequently updated). Semple et al. (2017) included a specimen *Spellenberg & Jewell* 9266 (NMC) from Chihuahua, Mexico, in a multivariate study of subsect. *Thrysiflorae* and this was placed a posteriori into a position between *S. petiolaris* (51% probability to this species in the first analysis and 64% in the second analysis) and *S. orientalis* (42% probability in the first analysis) and S. capulinensis (34% in the second analysis) and with low probabilities to *S. wrightii* (0% in the first analysis and 1% in the second analysis). Early in the multivariate study in 2007, the specimen had been set aside as a possible new species and the results of the multivariate study supported this conclusion.

SOLIDAGO SPELLENBERGII Semple, **sp. nov.** TYPE: **MEXICO. Chihuahua**. Mpio. Ocampo, Parque Nacional de Cascada Basaseachic, along trail down a SW-facing slope to base of falls, moderately open, with *Quercus, Pinus*, ca. 1800 m, 11 Sep 1987, *R. Spellenberg & D. Jewell 9266* (holotype: NMC; isotype: MEXU, not seen).

Similar to *Solidago petiolaris* but the lower mid stem leaves narrower, larger, and with a longer petiole than in that species and the inflorescence branching generally more open and long-branched; ovary/immature cypselae body very sparsely strigose. Similar to *Solidago wrighti* but stem leaves narrower, larger, and more membranous and ovary/immature cypselae body much less hairy.

Plants 96 cm; caudices branched, thick, and woody. **Stems** 1–3, simple, sparsely short villose-puberulent proximally to moderately densely so in array. **Leaves:** proximal dehisced by flowering, cauline **90**–110 × 14–17 mm, petiolate 4-10 mm, well differentiated, blades narrowly oblanceolate, sparsely puberulent on adaxial faces more so on veins of abaxial faces, margins entire proximally to 2-5 teeth distally, ciliate, reduced distally, entire; much reduced arrays. **Heads** 60, not secund, in open thyrsiform-paniculiform arrays, 20 × 16 cm, proximal branches much elongated 12–15 cm, not secund, diverging to ascending. **Peduncles** 10–18 mm, densely short villous-canescent, sparsely stipitate-glandular; bracts small, few, grading into phyllaries. **Involucres** campanulate, 6–7 mm. **Phyllaries** in 2--3 series, outer ca ½ the length of the inner, linear lanceolate, long attenuate, sparsely strigose, especially distally, sparsely to moderate minutely stipitate-glandular, +/- viscid.

Ray florets 6–7; laminae ca. 4–4.5 × 0.7–1.1 mm, yellow. **Disc florets** 10–15; corollas ca 3.2 mm, lobes ca. 1 mm; ovary 1.2-1.5 mm at anthesis. **Cypselae** (immature) somewhat compressed obconic, 2–2.5 mm, very sparsely short-strigose; **pappi** ca. 4 mm at anthesis; mature cypselae not seen. **Chromosome number** unknown.

Flowering September. Open oak-pine woods and rocky open slopes, disturbed ground; ca. 1800 m; Parque Nacional de Cascada Basaseachic, Chihuahua, Mexico.

The species is only known from the holotype collection. It is named in honor of the botanist Richard W. Spellenberg, Emeritus Curator of New Mexico State University Herbarium (NMC).

The multivariate study of subsect. *Thrysiflorae* (Semple et al. 2017) included four additional collections from the same general area of Mexico. *Spellenberg & Spellenberg 7926* (NMC) from S of the village of Basaseachic along the trail leading to Cascada was included in the *Solidago wrightii* a priori group and had much broader upper stem leaves than the holotype of *S. spellenbergii* and moderately strigose ovaries/fruit bodies; it was assigned a posteriori to *S. petiolaris* with 47% probability and to *S. wrightii* with 45% probability in the six species analysis and into *S. petiolaris* with 51% and *S. wrightii* with 49% in the four species analysis. *Nesom & Vorobik 5545* (TEX; Fig. 5) from the confluence of Rio Basaseachic and Rio Durazno had broader mid and upper stem leaves and sparsely strigose ovaries/fruit bodies: it was included a posteriori and assigned to *S. petiolaris* with 71% probability and 24% to *S. wrightii* in the first analysis and to *S. petiolaris* with 78% probability and 20% to *S. wrightii* in the second analysis. *Bye 9883* (NMC) from E of Yecora, Sonora, Mexico to the NW of Basaseachic was included in the *S. wrightii* a priori group and placed a posteriori into that group 85% probability and 87% probability in the two analyses; it had broader thicker leaves than the holotype of *S. spellenbergii*. *Van Devender et al. 98-636* (NMC) also from E of Yecora, Sonora was included in the *S. wrightii* a priori group and placed a posteriori into that group with 99% probability and 100% probability in the two analyses; it had small glandular and somewhat hairy leaves on small shoots. All four collections looked like more typical *S. wrightii* and none had leaves like those of the holotype of *S. spellenbergii*. All four collections were annotated as *S. wrightii* by the author. Guy Nesom (pers. comm.) observed that *S. wrightii* is "relatively common" in the Basaseachic area and noted that "other species endemic within the canyon mostly occur at its very bottom."

While most species in *Solidago* subsect. *Thyrsiflorae* occupy ranges that are allopatric or nearly allopatric, *S. spellenbergii* and *S. wrightii* appear to be sympatric in the local Basaseachic area. It is not clear from herbarium sheet habitat data whether or not the two are sympatric at the very local level or occur in slightly different habitats varying in edaphic or moisture conditions. Are the two species separated by ploidy level? Semple et al. (2017) noted that all counts for *S. wrightii* are diploid and that tetraploids are extremely rare in *S. petiolaris*. Is *S. spellenbergii* tetraploid? The lengths of floral parts often show differences correlated with ploidy level in *Solidago*, and thus involucre height, disc corolla length, ovaries/fruit bodies length at ca. anthesis, and pappus bristle lengths might indicate a ploidy difference between *S. spellenbergii* and *S. wrightii*. The values of each of these traits for *S. spellenbergii* fall within the range of variation of *S. wrightii* and thus do not indicate, but do not preclude, a difference in ploidy level.

A key to all taxa in *Solidago* subsect. *Thyrsiflorae* including *S. spellenbergii* is included and the end of the multivariate analysis and discussion in Semple et al. (2017)

ACKNOWLEDGEMENTS

permission to dissect heads of selected specimens: LL, NMC, TEX, and WAT in MT (Thiers continuously updated). The following students assisted in recording location data and collecting morphological data on specimens of *Solidago* subsect. *Thyrsiflorae*: Andrew Lam, Yunfei Ma, Urva Naik, Naomi Steenhof, and Lan Tong.

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Figure 1. Holotype of *Solidago spellenbergii* (*Spellenberg & Jewell 9266*) from Parque Nacional de Cascada Basaseachic, Chinhuahua, Mexico.
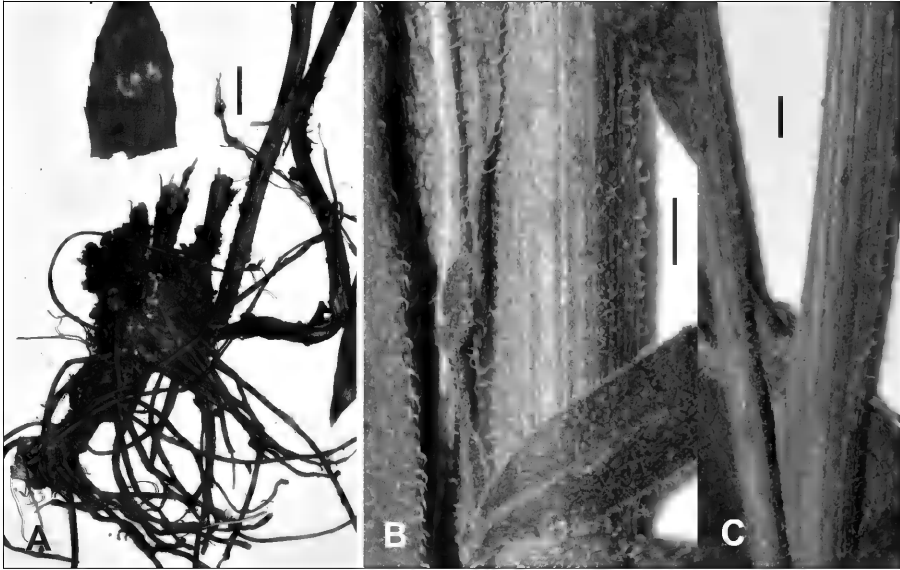
Figure 2. Details of holotype of *Solidago spellenbergii*: stems. A. Portion of rootstock and lower stems, some 1-2 seasons old. B. Upper stem. C. Stem in lower inflorescence. Scale bar = 1 cm in A; = 1 mm in B and C.
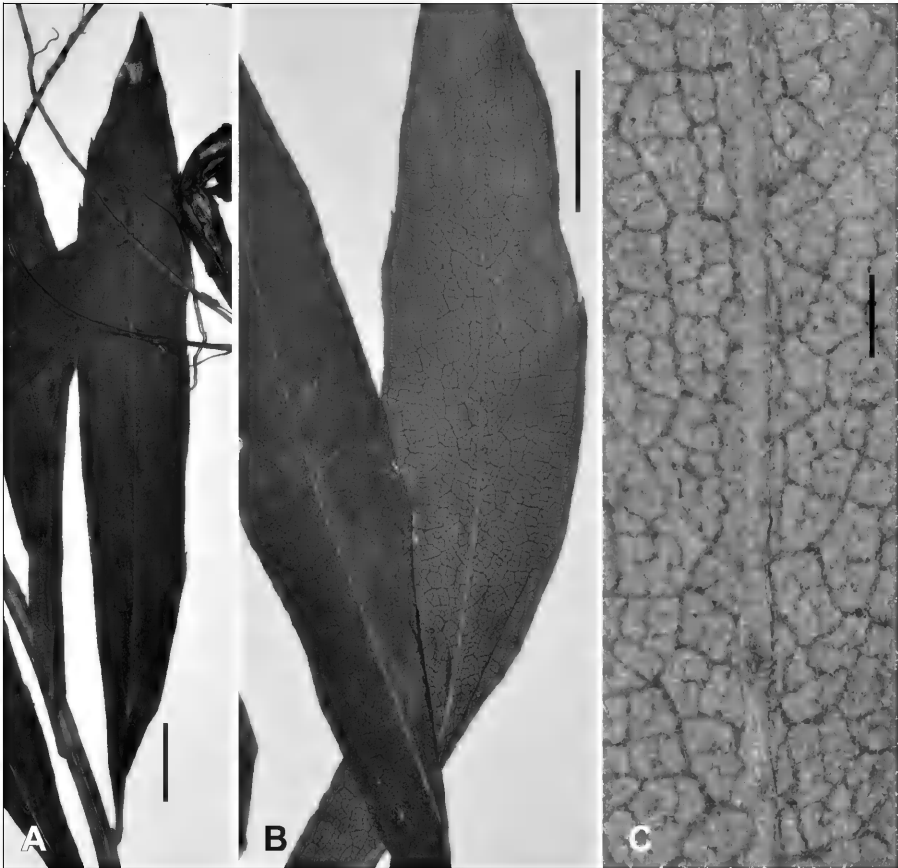
Figure 3. Details of holotype of *Solidago spellenbergii*: leaves. A. Mid stem leaf, adaxial surface. B. Upper stem. C. Mid stem leaf midvein at upper mid portion of leaf. Scale bar = 1 cm in A and B; = 1 mm in C.

Figure 4. Details of holotype of *Solidago spellenbergii*: heads and florets. A. Heads. B. Phyllaries. C. Ray floret. D. Disc florets at and post anthesis. Scale bars = 1 mm.

Figure 5. *Solidago wrightii* (*Nesom & Vorobik 5545* TEX) from Parque Nacional de Cascada Basaseachic, Chinhuahua, Mexico.

SOLIDAGO CORRELLII (ASTERACEAE: ASTEREAE), A NEW SPECIES FROM THE GUADALUPE MOUNTAIN REGION

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ABSTRACT

A new species, **Solidago correllii** Semple, is described from the Guadalupe Mountains of New Mexico and Texas. The holotype is *Correll & Johnston 19150* (LL) from McKittrick Canyon. It represents the same taxon (with a different type) earlier named as *Solidago wrightii* var. *guadalupensis* Nesom. The new species is named in honor of the late Donovan S. Correll.

Nesom (2008) described *Solidago wrightii* A. Gray var. *guadalupensis* Nesom and noted that it showed morphological affinities to *S. petiolaris* Ait. While first working on a multivariate analysis of all of *Solidago* subsect. *Thyrsiflorae* A. Gray in 2007, the author set aside several distinctive collections from the Guadalupe Mountains in Texas that might have been a new species. As the multivariate study progressed and sample sizes for taxa increased, it became obvious that these few Guadalupe Mountains collections belonged in the same taxon as those treated as Nesom's var. *gualalupensis*, but at species rank as indicated by the results of multivariate analyses (Semple et al. 2017). The higher rank is recognized here, using a different epithet and different type.

SOLIDAGO CORRELLII Semple, **sp. nov.** **TYPE**: **USA**. **Texas**: Culberson Co.: Guadalupe Mtns., mouth of McKittrick Canyon, along stream, flowers yellow, 2 Jul 1958, *D.S. Correll & I.M. Johnston 19150* (holotype: LL). Figures 1-2.

Solidago wrightii A. Gray var. *guadalupensis* G.L. Nesom, Phytologia 90: 29. 2008. **TYPE**: **USA**. **Texas**. Culberson Co.: Guadalupe Mts., south McKittrick Canyon, 27 Sep 1962, *D.S. Correll & H. Correll 26048* (holotype: LL!; isotype: SMU, not seen).

Similar to *Solidago wrightii* but the proximal stem leaves narrowly oblanceolate, petiolate and often present at flowering, shiny, sometimes silvery, glabrous except margins, and the ovary/cypselae body sparsely strigose (Fig. 3).

Plants 25–80 cm; caudices branched, thick, and woody rhizomes short (Fig. 4). **Stems** 1–5+, simple, sparsely to densely finely puberulent proximally to densely so in arrays. **Leaves:** basal and proximal winged-petiolate, blade attenuating into the petiole; blades oblanceolate, largest to 30–85 × 0.8–10.5 mm, green to silvery, shiny, glabrous, margins sparsely to moderately serrate, strigose; often present on stem at flowering, new rosettes sometimes present; cauline petiolate or sessile, blades linear-lanceolate to linear-elliptic, largest 21–60 × 3.5–13 mm, reduced distally, margins entire or with 1-2 small serrations. **Heads** 1–30, not secund, in thyrsiform-paniculiform arrays 2-20 × 1.5–13 cm, sometimes compact and nearly as wide as tall and rounded, sometimes appearing almost rounded corymbiform, proximal branches sometimes much elongate, not secund, ascending. **Peduncles** 5–2.5 mm, moderately to densely short hispid-canescent, somewhat viscid, stipitate glands minute; bracts small, linear 3-10, grading into phyllaries. **Involucres** campanulate, 3.5–6(–8) mm. **Phyllaries** in 3–4 series, unequal, linear lanceolate, acute to attenuate, sparsely to moderately viscid, especially distally, stipitate glands minute. **Ray florets** 5–13(–18); laminae ca. 3–7 × 0.5–2.2 mm, yellow. **Disc**

florets 5–25(–40); corollas 3.5–5.5 mm, lobes 0.5–1.8 mm. **Cypselae** 1.5–2.5 mm, +/- moderately short-strigose; **pappi** 3–4.6 mm. $2n = 18$.

Flowering late Jun–Sep. Open oak-pine woods and rocky limestone open ridges and slopes, gravelly stream beds; 1340–2300 m; Guadalupe Mts., N.Mex., Tex.

The species is named in honor of Donovan S. Correll, who collected many of the specimens examined and whose manual of the Texas flora with M.C. Johston (Correll & Johnston 1970) was a constant guide during the author's field work in Texas in the earlier 1970s.

Rarely a collection of *Solidago correllii* included basal rosettes (*Ward 84-028* NMC; Fig. 5). The holotype of *S. wrightii* var. *guadalupensis*, *Correll & Correll 26048* (LL), does not include basal rosettes or the lowest stem leaves; the main stem is also damaged and bears two elongated lateral branches each with an inflorescence. While the name *S. correllii* could have been based on the same holotype as *S. wrightii* var. *guadalupensis*, the new type *Correll & Johnston 19150* (LL) includes the lowest stem leaves and some persistent leaf bases (Fig. 2E) and undamaged stems. It was selected as the holotype for these features and because it was placed a posteriori into the *S. correllii* group with 100% probability in the multivariate study presented in detail in the sister paper by Semple et al. (2017). The lowest leaf is small and senescent. The persistent leaf bases also present on the small upper portion of the rootstook may be phylogenetically significant because they may indicate a relationship between *S.* subsect. *Thyrsiflorae* and *S.* sect. *Ptarmicoidei* (House) Semple & Gandhi, whose species consistently have persistent leaf bases. *Ward 84-028* (NMC) also has persistent senescent leaves, and upon first examining the collection I thought it might be a new species in sect. *Ptarmicoides* related to *S. nitidula* Torr. & A. Gray. The intuitive phylogeny of *Solidago* (Semple 2016) shows two possible origins for sect. *Ptarmicoides*, one as the basal branch in the genus and second as a basal branch off the subsect. *Thyrsiflorae* clade. Molecular data is needed to clarify whether or not either of these possibilities is likely.

Semple et al. (2001) reported a chromosome number of $2n = 18$ for *Solidago correllii* under the name *S. wrightii* (*Semple & Heard 8185*, vouchers in BRIT, MO, NMC, US, and WAT), which is corrected here.

Additional collections examined: USA. **New Mexico.** Eddy Co.: Guadalupe Mtns, about 48 km (by air) SE of Carlsbad at Sitting Bull Falls, reached by NM-137, canyon bottom, *R. Spellenberg & M. Spellenberg 4199* (NMC); Lincoln Natl Forest, Devils Den Canyon, S to end of rim road 540, then 2 mi SSW on Forest Trail 202, in mine tailings on NNE facing slopes, *Brunt 0009* (NMC). Lincoln Co.: *Skehan 70* (NMC). **Texas.** Culberson Co.: Guadalupe Mts. Natl Park, along Bear Canyon, *Semple & Heard 8169* (WAT); jct of Bear Canyon Trail and Bowl Trail, *Semple & Heard 8178* (WAT). Bowl Trail, *Semple & Heard 8185* (BRIT, MO, NMC, US, WAT; Fig. 6); above McKittrick Canyon, *Moore & Steyermark 3629* (LL); McKittrick Canyon, 5 mi NW of US-62/180 intersection with access road to canyon, 2.5 mi (by foot) into canyon, just W of lodge ruins, *Ward 84-028* (NMC, NY; Fig. 5); mouth of McKittrick Canyon, *Correll & Johnston 19150* (LL); N McKittrick Canyon, *Correll 13948* (LL); S McKittrick Canyon, *Warnock 10972* (LL); 2.4 km S, 1.0 km W of Pratt Lodge, ca. 1/2 km SE of Turtle Rock, *Burgess 3710* (TEX); S fork of McKittrick Canyon, *Correll & Correll 26048* (LL, SMU), *Correll & Hanson 29808* (LL). *Solidag*o aff. *S. correllii*: **USA. Texas**: Jeff Davis Co., at NE tip of Bear Mountain, ca. 0.8-1.0 mi. air mi. SSW of summit of Bear Cave Mtn., *Carr, Karges, Cook, & Poole 16911* (TEX). Nesom (2008) listed additional collections under the name *S. wrightii* var. *guadalupensis*.

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in MT (Thiers, continuously updated). The following students assisted in recording location data and collecting morphological data on specimens of *Solidago subsect. Thyrsiflorae*: Andrew Lam, Yunfei Ma, Urva Naik, Naomi Steenhof, and Lan Tong. Guy Nesom is thanked for his helpful comments on several drafts of this paper.

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Thiers, B. [continuously updated]. Index Herbariorum: A global directory of public herbaria and associated staff. Virtual Herbarium, New York Botanical Garden. <http://sciweb.nybg.org/science2/IndexHerbariorum.asp>

Figure 1. Holotype of *Solidago correllii* Semple; *Correll & Johnston 19150* (LL).
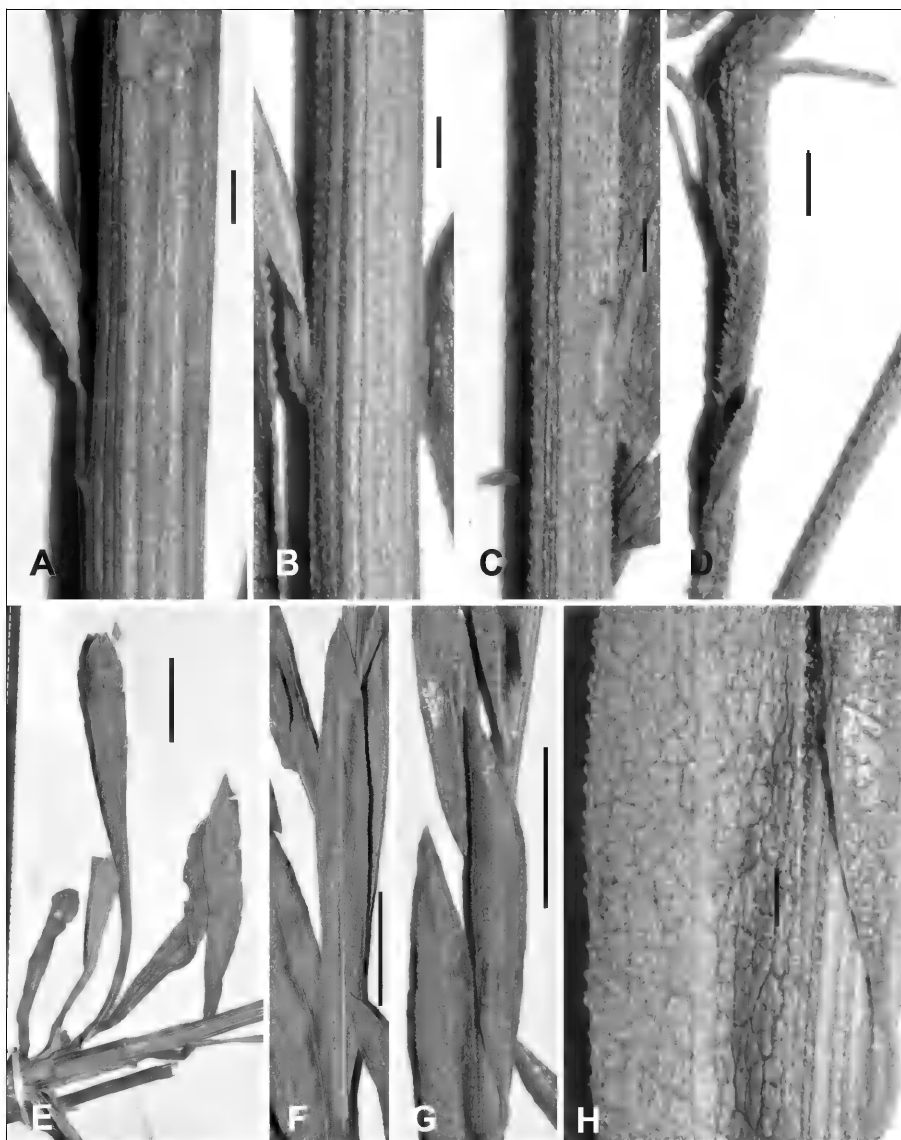
Figure 2. Details of holotype of *Solidago correllii*: stems and leaves. **A-C.** Lower, mid and upper stems. **D.** Peduncles. **E.** Lower stem leaves from base of stem. **F.** Mid stem leaf. **G.** Upper stem leaves. **H.** Upper stem leaf, adaxial surface. Scale bar = 1 mm in A-D, H; = 1 cm in E-G.
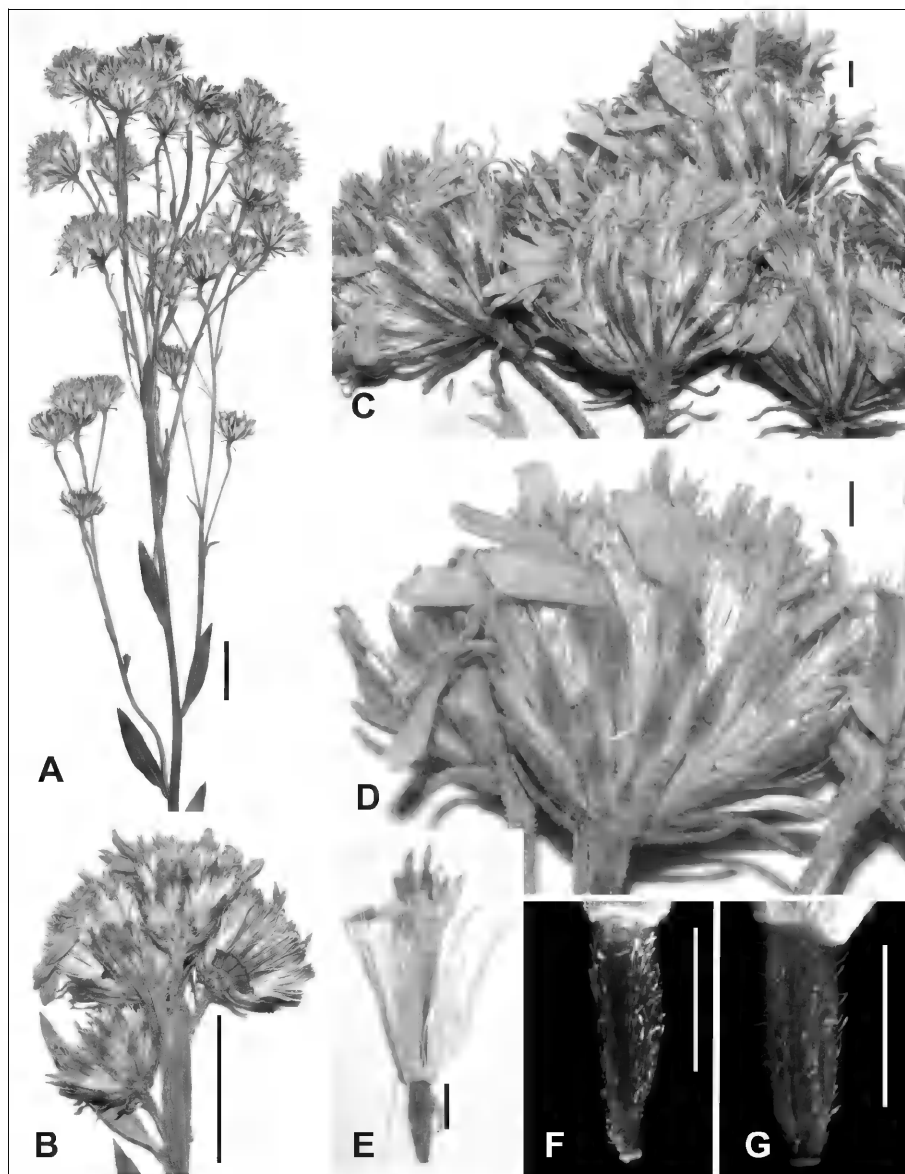
Figure 3. Details of holotype and other collections of *Solidago correllii*: heads and florets. **A.** Holotype, inflorescence. **B.** *Moore & Steyermark 3629* (LL), small inflorescence. **C-D.** Holotype, heads. **E.** Holotype, disc floret. **F-G.** *Correll 13948* (LL) and *Warnock 10972* (LL), ray and disc floret ovaries. Scale bar = 1 cm in A-B; = 1 mm in C-G.
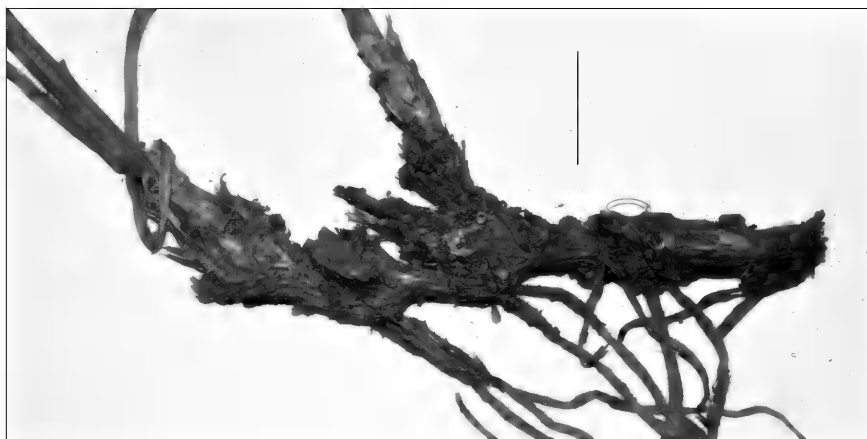
Figure 4. Details of addition specimens of *Solidago correllii*: rootstook, *Moore & Steyermark 3629* (LL). Scale bars = 1 cm.

Figure 5. Details of addition specimens of *Solidago correllii*: silvery gray-green basal rosette (A) and lower stem leaves (A, B), *Ward 84-028* (NMC). Scale bars = 1 cm.

Figure 6. *Solidago correllii* in the field, Guadalupe Mts. National Park, the Bowl Trail, 7880 ft. elev., *Semple & Heard 8185.* **A.** Habitat. **B.** Flowering heads.

A MULTIVARIATE MORPHOMETRIC ANALYSIS OF *SOLIDAGO* SUBSECT. THYRSIFLORAE (ASTERACEAE: ASTEREAE)

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ABSTRACT

A multivariate morphometric study of the goldenrod group *Solidago* subsect. *Thyrsiflorae* was conducted to assess the morphological differences among *Solidago buckleyi, S. capulinensis, S. correllii, S. orentialis,* S. *petiolaris, S. spellenbergii* and *S. wrightii,* and to compare the varieties within *S. petiolaris* and *S. wrightii.* Analyses of a matrix of 150 specimens by 39 traits provided significant support recognizing 7 species as well as for recognizing var. *angusta,* var. *petiolaris,* and var *wardii* in *S. petiolaris.* Varieties within *S. wrightii* were not recognized because the putative differences were based on continua of variation in phyllary gland and hair densities with no non-arbitrary way to split samples between densely glandular/non-hairy and non-glandular/densely hairy forms.

Solidago subsect. *Thyrsiflorae* includes 3-7 species depending upon the taxonomic treatment (Nesom 1989, 1990, 2008; Semple & Cook, 2006; Nesom & Lowrey 2011; Semple 2017 a, b; Semple 2017 frequently updated): *S. buckleyi* Torr. & A. Gray, *S. capulinensis* Cockerell & Andrews, *S. correllii* Semple, *S. orientalis* (Nesom) Nesom, *S. petiolaris* Ait., *S. spellenbergii* Semple, and *S. wrightii* A. Gray.

* **Solidago buckleyi** is generally distinguished by its large lower and mid stem leaves that are oblanceolate acuminate and obviously serrate (Figs. 1-2).

* **Solidago capulinensis** (Figs. 3-4) has generally not been recognized as a distinct species and was not included in Flora North America by Semple and Cook (2006). Nesom and Lowrey (2011) presented reasons for recognized the species.

* **Solidago correllii** is similar to both *S. petiolaris* and *S. wrightii* but differs in having often persistent lower stem leaves and rarely basal rosettes present at flowering (see Figs 1-4 in Semple 2017a). The lower stem leaves are narrowly oblanceolate tapering to a long petiole. Leaves can be rather silvery green when dried. Ovaries/fruit bodies are sparsely to moderately strigose. *Solidago correllii* was treated as *S. wrightii* var. *guadalupensis* Nesom by Nesom (2008) but was raised to species level and given a new name and type.

* **Solidago orientalis** is distinquished by it serrate stem leaves (Figs. 5-6). Nesom (1989) first described the taxon as *S. wrightii* var. *orientalis* Nesom but soon raised the taxon to species rank (Nesom 1990).

* **Solidago petiolaris** is distinguished by its stem leaves with very short (1-3 mm) petioles and the branching pattern of its infloresences. The species includes three sometime difficult to distinguish varieties that differ in leaf shape and indument traits and phyllary indument traits (Figs. 7-9). The var. *petiolaris* has broadly lanceolate-elliptic to ovate-elliptic usually entire leaves and has phyllaries that are non-glandular to very sparsely glandular and that are sparsely to densely strigose. The var. *angusta* (Torr. & A. Gray) A. Gray (Figs. 8-9) was first described as *S. angusta* Torr. & A. Gray (1842) defined as the name suggests by its narrow lanceolate leaves and later by its sparsely glandular resinous and not hairy phyllaries. The var. *wardii* (Britt.) Fern. was first described as *S. wardii* Britt.

Figure 1. *Solidago buckleyi, Palmer 31571a* (NY) Mine la Motte, Madison Co., Missouri.
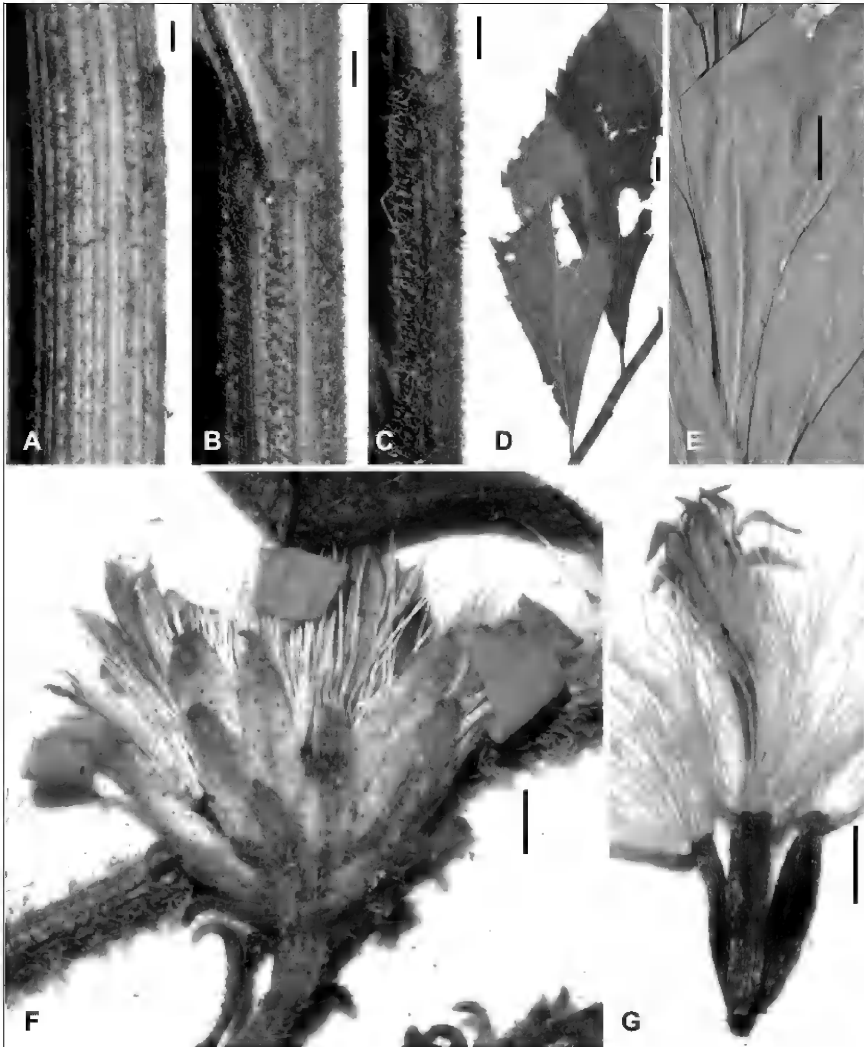
Figure 2.   Details of morphology of *Solidago buckleyi*.   **A-C.** Lower, mid and upper stem in inflorescence, *Keener 4013* (WAT).   **D.** Lower stem leaves, *Semple & Suripto 9936* (WAT).   **E.** Mid stem leaves, *Letterman s.n.* (NY).   **F.** Pressed head, Brant et al. 753 (WAT).   **H.** Disc floret cypselae, Eggleston 5397 (NY).   Scale bars = 1 mm in A-C, and F-G; = 1 cm in D-E.

Figure 3. *Solidago capulinensis*, *Lowrey 2190C* (UNM unmounted) from Mt. Capulin Nat. Monument, Union Co., New Mexico.

Figure 4. Details of morphology of *Solidago capulinensis*: *Lowrey 2190-B, -C, - E, -F* and *-4* (UNM unmounted). **A**. Basal of stem with new developing lateral shoots. **B**. Mid stem. **C**. Lower stem leaf. **D**. Mid stem leaves. **E**. Mid stem leaf, mid vein, abaxial surface. **F**. Heads. **G**. Disc floret cypselae. Scale bars = 1 mm in B, E, F-G; = 1 cm in A, C-D.
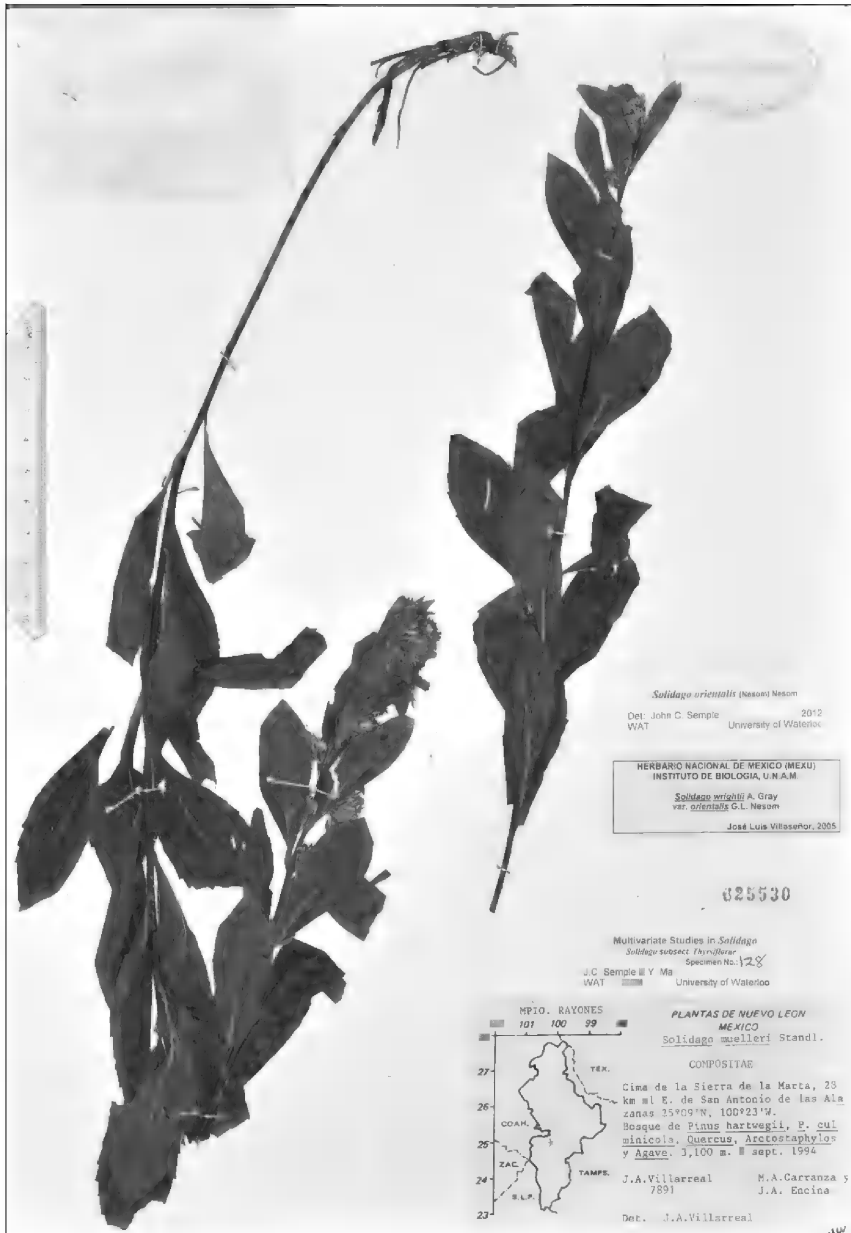
Figure 5. *Solidago orientalis*, *Villarreal 7891* (MEXU), Cima de la Sierra de la Marta, Nuevo Leon, Mexico.
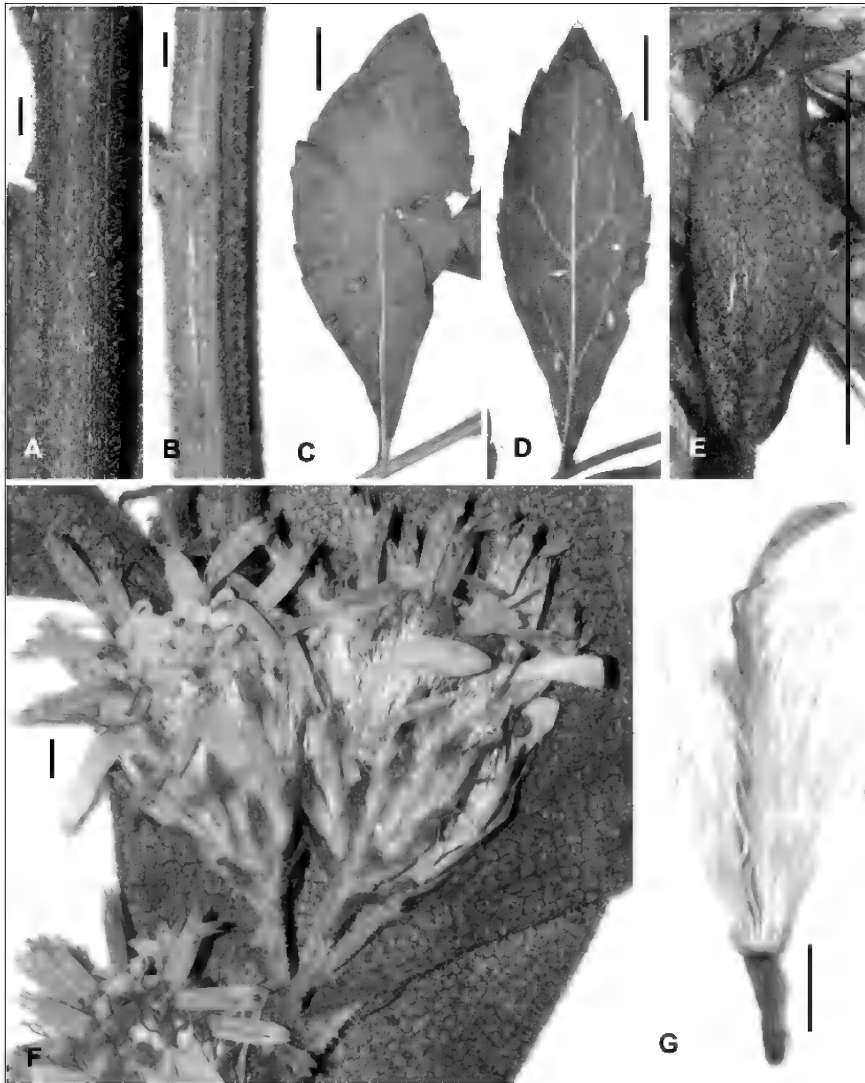
Figure 6. Details of morphology of *Solidago orientalis*: **A-B.** Mid stems; *Villarreal 7891* (MEXU) and *Hinton et al. 27489* (TEX).   **C-D.** Mid stem leaves; *Hinton et al. 27489* (TEX) and Hinton et al. *18613* (TEX).   **E.** Peduncle bract; *McDonald & Mayfield 2560* (MEXU).   **F.** Heads; *Hinton et al. 21617* (TEX).   **G.** Ray floret cypsela and post flowering ray floret corolla, immature; *Hinton et al. 18613* (TEX). Scale bars = 1 mm in A-B, F–G; = 1 cm in C-E.

and was defined by its lanceolate to broadly lanceolate leaves that are glabrous to sparsely strigose and phyllaries that are sparsely to densely strigose (Figs. 8-9). Application of the varietal names has varied in different floras or were not recognized. Britton (1901) keyed green leaved plants to *S. petiolaris* and silver leaved plants to *S. wardii*, but some of the silver leaved plants have more broadly lanceolate to ovate mid and upper stem leaves (Figs. 8F, 8I); such plants occur in the western Ozark Mts, and Ouachita Mts. in southwestern Missouri, western Arkansas, eastern Oklahoma and adjacent Texas. Fernald (1908) in making the combination var. *wardii* stated that these differed from typical *S. petiolaris* in having "firmer more glutinous and therefore more lustrous foliage." Nesom (1990) noted that the definition of var. *angusta* had shifted over time to define the taxon as having leaves that were "strongly glutinous, shiny, the lower surfaces glabrous or merely scabrous-hispidulous along the midrib and main veins" and involucres that were "granular glandular to glabrous" while var. *petiolaris* had leaves that were "scarely glutinous, not shiny, the lower surfaces densely spreading hairy to softly puberulent" and involuces "puberulent (often viscidulous) to occasionally glabrous. Nesom (1990) concluded that *S. wardii* should be treated as a synonym of *S. petiolaris*. Semple and Cook (2006) did not recognize varieties within *S. petiolaris* in the treatment of the species in Flora North America and listed the following as synonyms: *Aster lindheimeranus* (Scheele) Kuntze; *A. petiolaris* (Aiton) Kuntze; *Solidago angusta* Torrey & A. Gray*; S. harperi* Mackenzie ex Small; *S. lindheimeriana* Scheele; *S. milleriana* Mackenzie ex Small; *S. petiolaris* var. *angusta* (Torrey & A. Gray) A. Gray; *S. petiolaris* var. *squarrulosa* Torrey & A. Gray; *S. petiolaris* var. *wardii* (Britton) Fernald; *S. squarrulosa* (Torrey & A. Gray) Alph. Wood; *S. wardii* Britton. Yatskievych (2006) presented a useful summary of the problem of intergrading traits in his edition of the Flora of Missouri. Nesom (2008) discussed differences between the varieties and applications of the names and included maps showing differences in distribution of morphotypes. He applied the name var. *angusta* to plants with phyllaries that have slightly raised glands and no hairs (Figs. 9 C-E) regardless of whether the leaves are narrowly or broadly lanceolate to narrowly ovate (Figs. 8 F-I). Such plants occur from Missouri through Arkansas to Louisiana and west from southeastern Kansas to Texas and disjunct in northern Coahuila, Mexico. Phyllaries of var. *wardii* are obviously hairy (Fig. 9 H).

  * **Solidago spellenbergii** is distinguished from *S. wrightii* by having longer lanceolate leaves than typically found in the latter and ovaries/fruit bodies that are nearly glabrous (see Figs 1-3 in Semple 2017b). The species is known from a single collection and might be a local ecotype of *S. wrightii*.

  * **Solidago wrightii** is distinguished by its non-serrate stem leaves and inflorescences that are sometimes subcorymbiform and its moderately strigose ovaries/fruit bodies (Figs. 10-12). Several varieties have been recognized within the species but are not recognized here; *S. wrightii* var. *adenophora* Blake was distinguished by its upper leaves, stems and phyllaries being densely stipitate glandular and not hairy (Fig. 12I) while var. *wrightii* had sparsely to non-glandular upper leaves, stems, and phyllaries that were moderately to densely strigose (Fig. 12H). Kearney et al. (1960) recognized var. *adenophora* as a more southern form of the species in Arizona. Nesom (2008) concluded that there was considerable range of variation in the the numbers of hairs and glands on phyllaries and recognized the most glandular forms as f. *adenophora* (Blake) Nesom.

  The distributions of the seven species are overall allopatric, with some sympatry at the margins. *Solidago buckleyi* is native to the open woods in eastern Missouri, southern Illinois and Indiana, and north central Alabama (Fig. 13; Semple & Keener 2016). The species is sympatric with *S. petiolaris* in Missouri and Arkansas. *Solidago correllii* is the only species present in the Guadalupe Mountains of Texas and New Mexico but possibly occurs in the White Mountains further north in New Mexico (Fig. 13) where *S. wrightii* is more common (Nesom 2008, as *S. wrightii* var. *guadalupensis*) and in possibly further south in the Davis Mountains of trans-Pecos Texas. *Solidago orientalis* is native to the Sierra Madre Oriental of northeastern Mexico (Fig. 13; Nesom 1990) and is allopatric with other species in the subsection.

Figure 7. *Solidago petiolaris*, *Freeman 56744* (NCU) from Rutherford Co., North Carolina.
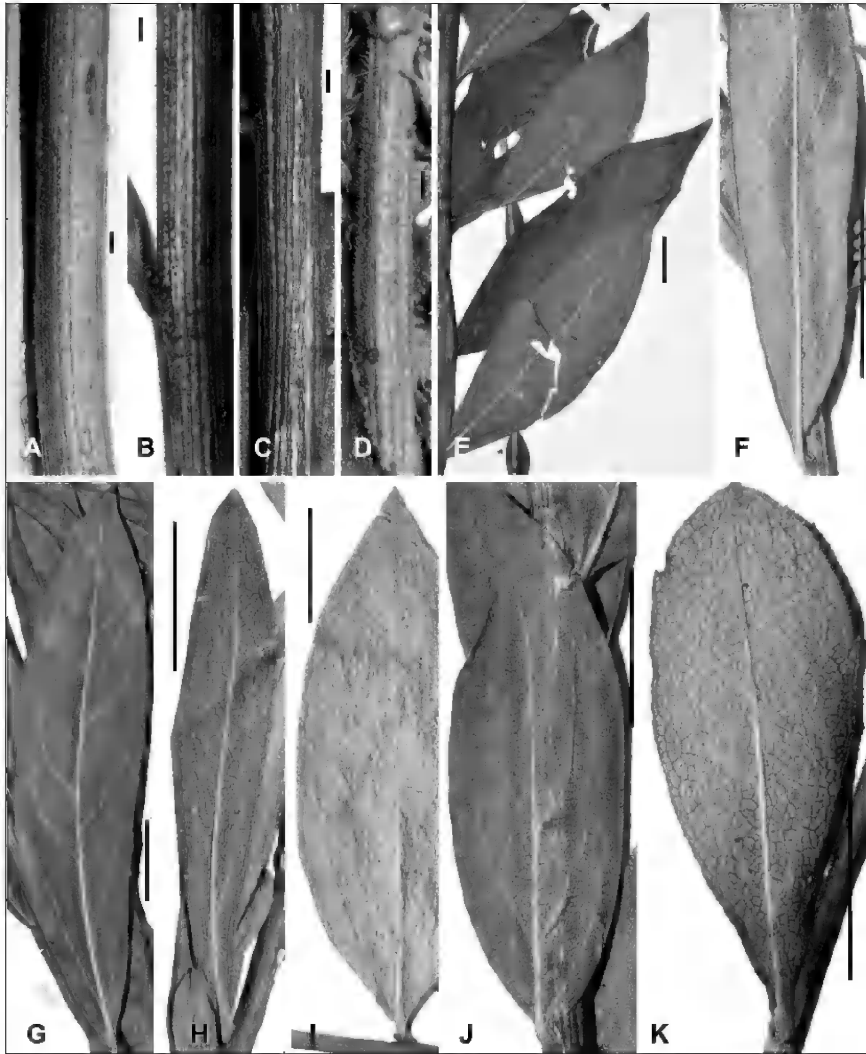
Figure 8.   Details of morphology of *Solidago petiolaris*: stems and leaves.   **A.** Lower stem, *Ward s.n.* (GH isotype of *S. wardii*).   **B-C.** Mid stems; var. *petiolaris*, *Jones 22337* (NCU) and var. *angusta*, *Thomas et al. 68478* (WAT).   **D.** Stem in inflorescence, var. *wardii*, *Drake 183* (TEX).   **E.** Lower mid stem leaves, var. *petiolaris*, *Ahles 36076* (NCU).   **F.** Upper stem leaf, var. *angusta*, *Semple & Heard 8274* (WAT).   **G-H.** Mid stem leaves, var. *angusta*, *Thomas 138410* (LSU) and *Henrickson 11471* (LL).   **I-J.** Upper mid stem leaves, var. *angusta*, *Correll 26345* (LL) and var. *petiolaris*, *Kral 41739* (WAT).   **K.**   Serrate secondary branch leaf, var. *petiolaris*, *Radford 30544* (NCU). Scale bars = 1 cm.
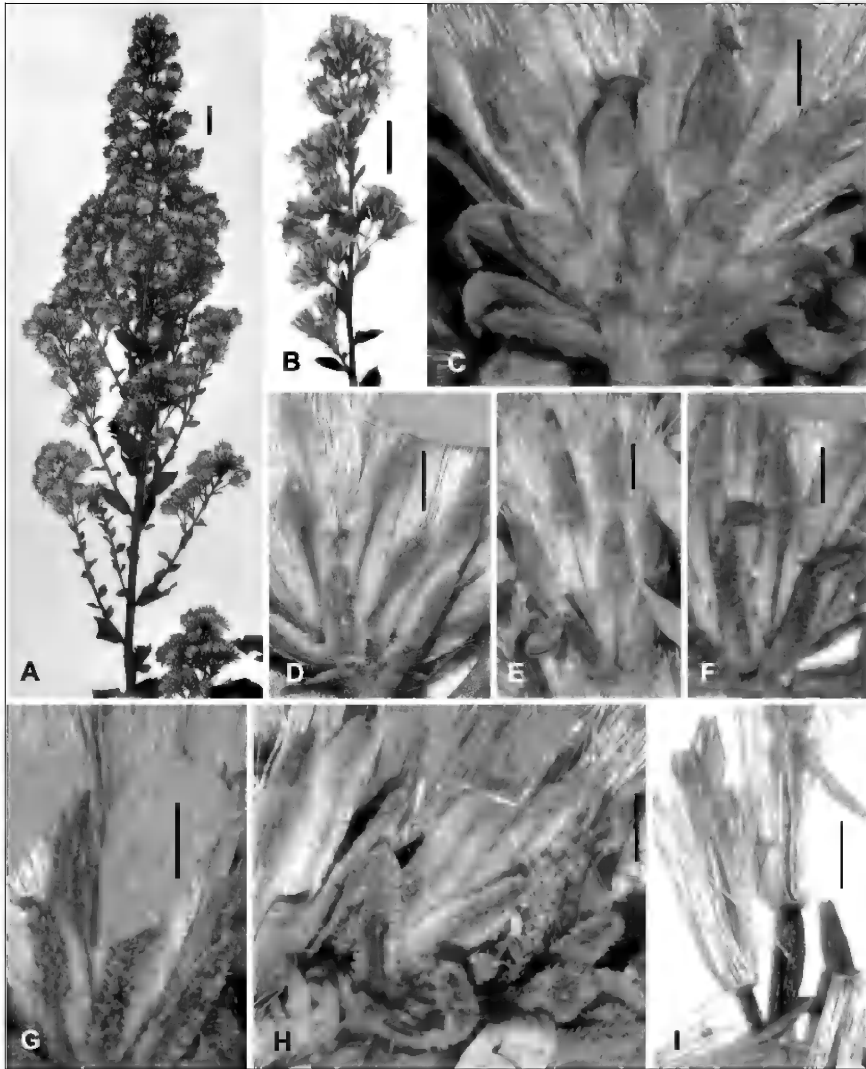
Figure 9. Details of morphology of *Solidago petiolaris*: floral traits. **A-B.** Inflorescences, var. *petiolaris*, wide, *Radford 29536* (NCU) and small, *Semple & Chmielewski 6186* (WAT). **C-H.** Phyllaries. **C-E.** Resinous, glandular. **C.** Broad leaved var. *angusta, Semple & Heard 8268* (WAT). **D.** Ovate leaved var. *angusta, Correll 26345* (LL). **E.** Var. *angusta, Thomas 138410* (LSU). **F-G.** Var. *petiolaris, Harbison s.n.* (NCU) and *Marsh 55-21* (TEX). **H.** Isotype of var. *wardii, Ward s.n.* (GH). **I.** Disc floret immature cypselae, var. *wardii, Taylor 23743* (LSU). Scale bars = 1 mm in C-I = 1 cm in A-B.

Figure 10. *Solidago wrightii, Wooton & Standley 3688* (NMC) from Lincoln Co., New Mexico.

Figure 11. *Solidago wrightii, Semple & Heard 7988* (WAT) from Cochise Co., Arizona.
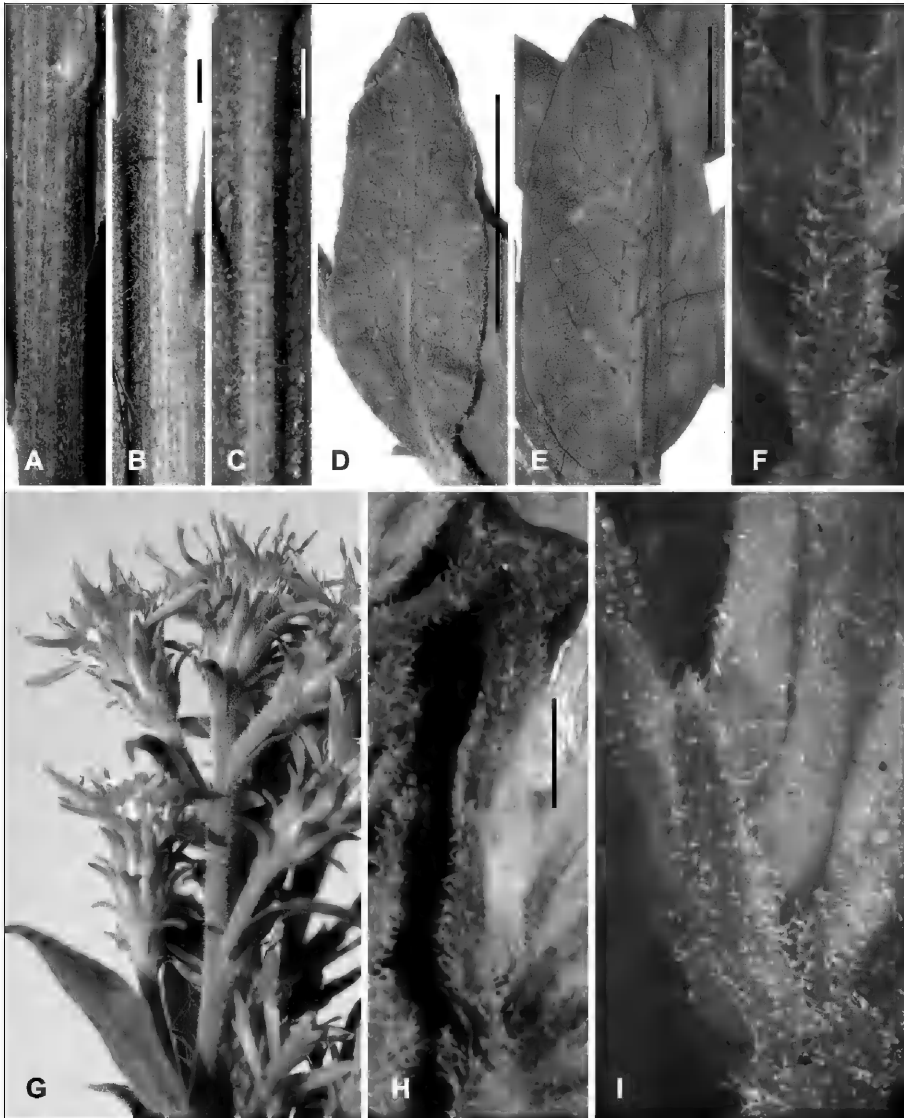
Figure 12. Details of morphology of *Solidago wrightii*. **A-B**. Mid and upper stems, hairy, *Semple & Heard 8038* (WAT) and *Sherman et al 202* (WAT). **C.** Upper stem, glandular, *Van Devender 98-636* (NMC). **D-E.** Upper stem leaves, hairy, *Semple & Chmielewski 9000* (WAT), and glandular, *Bye 9883* (NMC). **F.** Peduncle bract, hairy, *Semple & Heard 8038* (WAT). **G.** Fresh heads, glandular, *Semple & Heard 7930* (WAT). **H.** Phyllaries, hairy, *Semple & Heard 8038* (WAT). **I.** Phyllaries, glandular, *Semple & Heard 7988* (WAT). Scale bars = 1 mm in A-C, and H; = 1 cm in D-E.

Solidago petiolaris is native to the southern USA from eastern New Mexico to North Carolina and south to Texas into northern Mexico in rocky soils in open woods and disturbed slopes (Fig. 13): var. *petiolaris* occurs mostly east of the Missisippi River with some collections coming from eastern Texas; var. *angusta*, occurs from Missouri and southeastern Kansas south to Louisiana and northeastern Texas with scattered populations in eastern and southern Oklahoma and across Texas in disjunct areas to the mountains of northern Coahuila, Mexico; var. *wardii* occurs from northeastern New Mexico to northeastern Kansas and south to Panhandle and central Texas (Nesom 2008). *Solidago spellenbergii* is known only from the type location in Parque Nacional de Cascada Basaseachic, western Chihuahua, Mexico. It was been collected along a trail on the slope to the base of the falls in moderately open woods with *Quercus* and *Pinus*. *Solidago wrightii* is native to the mountains of Arizona, New Mexico, and trans-Pecos Texas in the USA and the eastern portions of the Sierra Madre Occidental in Sonora, western Chihuahua, and Durango and southwestern Coahuila in Mexico (Fig 13). It also occurs on the high plains in northeastern New Mexico and southeastern Colorado (Nesom 2008).

Nesom (1993) included *Solidago hintoniorum* Nesom and *S. speciosa* Nutt. (including *S. harperi* Mackenzie and *S. jejunifolia* Steele) in subsect. *Thyrsiflorae*, but these were not included in subsect. *Thyrsiflorae* by Semple (2017 frequently updated). *Solidago hintoniorum* has traits typical of subsect. *Nemorales* including large lower stem leaves. *Solidago speciosa* and *S. jejunifolia* are typical members of subsect. *Squarrosae* and have large lower stem leaves (Semple et al. 2017).
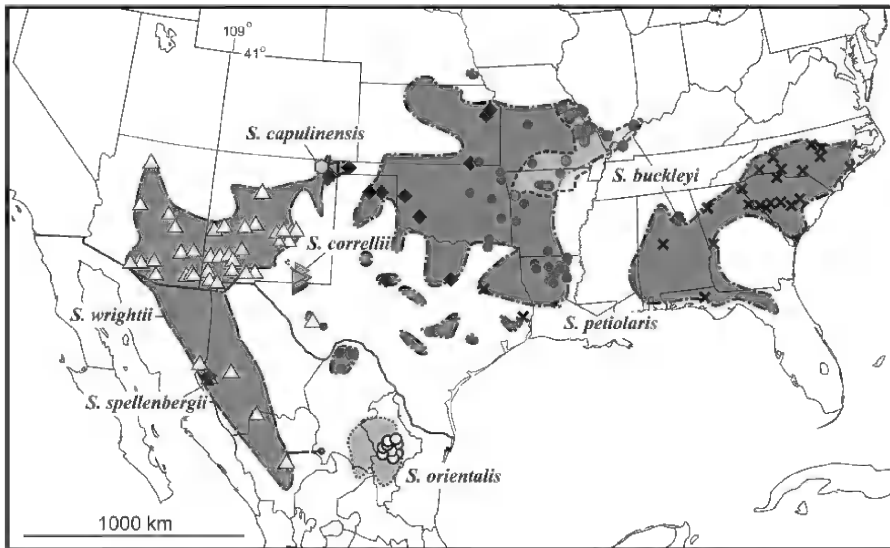
Figure 13. Distribution of 150 specimens included in the multivariate analyses of *Solidago* subsect. *Thyrsiflorae*: *S. buckleyi* (red dots), *S. capulinensis* (pink polygon), *S. correllii* (gray right-pointing triangles), *S. orientalis* (white-filled black circles), *S. petiolaris* (var. *petiolaris*, black crosses; var. *angusta* with more or less glandular resinous phyllaries and includes some silver leaved specimens, green dots; var. *wardii* with hairy phyllaries, black diamonds), *S. spellenbergii* (green star); *S. wrightii* (white-filled blue triangles).

All chromosome numbers reported for taxa in *Solidago* subsect. *Thyrsiflorae* are diploid, 2n=9II or 2n=18, with one exception. Diploid counts have been reported for *S. correllii* (Semple et al. 2001 as *S. wrightii*; corrected in Semple 2017a), *S. petiolaris* (Beaudry 1963, Semple et al. 1981; Semple et al. 1993; Semple & Cook 2004; Semple, Cook, & Owen 2015; Morton et al. in press; unpublished) and *S. wrightii* (Turner et al. 1962; Beaudry 1969; Anderson et al., 1974; Keil & Pinkava 1979, 1981; Windham & Schaak 1983; Ward & Spellenberg 1986; Semple & Chmielewski 1987; Keil et al. 1988; Semple et al. 1992, 2001; Morton et al. in press; unpublished). Semple et al. (1992) reported the single tetraploid count for *S. petiolaris*; the identity of the voucher *Semple et al. 3044* (WAT) from Richmond Co., North Carolina, is confirmed below in the multivariate analyses, but the count itself cannot be confirmed to be from the field collected plant used as the voucher. Semple and Cook (2004) corrected the misidentification of two reports of tetraploids for *S. petiolaris* (Semple et al. 1984) to *S. leavenworthii*. Chromosome numbers have not been reported for *S. buckleyi*, *S. capulinensis*, *S. orientalis*, and *S. spellenbergii*.

The purpose of this study was to determine statistical support for recognizing the species and varieties proposed within *Solidago* subsect. *Thyrsiflorae*, the levels of distinctiveness among the taxa, and what technical traits could be used to separate taxa besides those used to define the taxa as a priori groups.

MATERIAL AND METHODS

Herbarium specimens were borrowed and examined from the following herbaria (GH, LL, LSU, MEXU, NY, NCU, NMC, TEX, UNM, and WAT in MT; Thiers continuously updated). More than 700 specimens were examined, from which 150 were chosen and measured for the statistical analyses based on completeness, maturity, and geographical distribution (17 specimens of *Solidago buckleyi*, 10 of *S. capulinesis*, 13 of *S. correllii*, 7 of *S. orientalis*, 66 of *S. petiolaris*, 1 of *S. spellenbergii* included in a posteriori analyses, and 36 of *S. wrightii*). In total, 20 vegetative and 19 floral traits were scored for the final analyses (Table 1). Preliminary analyses not reported below included additional stem, leaf and phyllary indument traits scored on a smaller number of specimens.

All analyses were performed using SYSTAT v.10 (SPSS 2000). Details on the methodology were presented in Semple et al. (2016) and are not repeated here. Five analyses were performed. In the first analysis, *Solidago buckleyi*, *S. capulinensis*, *S. correllii*, *S. orientalis*, *S. petiolaris*, and *S. wrightii* were included in a STEPWISE discriminant analysis and a COMPLETE with six traits, plus one specimen of *S. spellenbergii* included a posteriori. In the second analysis, *S. capulinensis*, *S. correllii*, *S. petiolaris*, and *S. wrightii* were included in a STEPWISE discriminant analysis plus one specimen of *S. spellenbergii* included a posteriori. In the third analysis, *S. petiolaris* var. *angusta¸ S. petiolaris* var. *petiolaris*, and *S. petiolaris* var. *wardii*, were included in a STEPWISE discriminant analysis using Nesom's (2008) limits of the varieties with var. *angusta* including specimens with hairless phyllaries with either glands or resin. In the fourth analysis, *S. petiolaris* var. *angusta¸ S. petiolaris* var. *petiolaris*, and *S. petiolaris* var. *wardii*, were included in a STEPWISE discriminant analysis using alternative limits of the varieties with var. *angusta* defined by having narrow leaves and var. *wardii* by having broader leaves and phyllaries that were either hairy or not hairy. In the fifth analysis, the numbers of glands and hairs on upper stem leaves and phyllaries of specimens of *S. wrightii* were investigated and several ways including a STEPWISE analysis. A number of additional preliminary analyses were run but are not reported here.

Table 1. Traits scored for the multivariate analyses of 150 specimens of *Solidago* subsect. *Thyrsiflorsae.*

Abbreviation	Description of trait scored
STEMHT	Stem height measured from the stem base to tip (cm)
BLFLN	Basal rosette leaf length including petiole (mm)
BLFPETLN	Basal rosette leaf petiole length (not scored if winged margins broad)
BLFWD	Basal rosette leaf width measured at the widest point (mm)
BLFWTOE	Basal rosette leaf measured from the widest point to the end (mm)
BLFSER	Basal rosette leaf–number of serrations on 1 side of margin
LLFLN	Lower leaf length measured from the leaf base to tip (mm)
LLFWD	Lower leaf width measured at the widest point (mm)
LLFWTOE	Lower leaf measured from the widest point to the end (mm)
LLFSER	Lower leaf dentation–number of serrations of lower leaf
MLFLN	Mid leaf length measured from the leaf base to tip (mm)
MLFWD	Mid leaf width measured at the widest point (mm)
MLFWTOE	Mid leaf measured from the widest point to the end (mm)
MLFSER	Mid leaf dentation–number of serrations of mid leaf
LEAGMM	Number of glands per mm^2 on upper stem leaf upper surface*
LEAHMM	Number of hairs per mm^2 on upper stem leaf upper surface*
ULFLN	Upper leaf length measured form the leaf base to tip (mm)
ULFWD	Upper leaf width measured at the widest point (mm)
ULFWTOE	Upper leaf measured from the widest point to the end (mm)
ULFSER	Upper leaf dentation–number of serrations of upper leaf
CAPL	Length of inflorescence (cm)
CAPW	Width of inflorescence (cm)
INVOLHT	Involucre height at anthesis (mm)
OPHYLN	Outer phyllary length (mm)
PHYGD	Number of glands per mm^2 on mid series phyllary distal half
PHYHAIR	Number of hairs per mm^2 on mid series phyllary distal half
OPHYLW	Outer phyllary width (mm)
IPHYLN	Inner phyllary length (mm)
IPHYLW	Inner phyllary width (mm)
RAYNUM	Number of ray florets per head
RSTRAPLN	Ray strap length top of the corolla tube to the tip of the strap (mm)
RSTRAPWD	Ray strap width measured at the widest point (mm)
RACHLN	Ray floret ovary/fruit body length at anthesis (mm)
RPAPLN	Ray floret pappus length at anthesis (mm)
DCORLN	Disc floret corolla length from the base to tip of the corolla lobes (mm)
DLOBLN	Disc floret corolla lobe length lobe (mm)
DACHLN	Disc floret ovary/fruit body length at anthesis (mm)
DPAPLN	Disc floret pappus length at anthesis (mm)
DACHPUB	Number of hairs on disc floret ovary/fruit body

*Preliminary analyses only

RESULTS

Six species level a priori groups taxa analysis

The Pearson correlation matrix yielded r > |0.7| for most pairs of leaf traits reducing the number to be used to the number of mid stem leaf margin serrations. Basal rosette leaves were present in only a few specimens of *S. correllii* and a single specimen of *S. wrightii* and were not included in the analyses. Lower stem leaves were present on many specimens but were not included in the analyses because their traits correlated highly among themselves and with mid stem leaf traits. Among the floral traits scored, only ray floret pappus length and disc floret pappus length correlated highly; the latter was included in the analyses.

In the COMPLETE discriminant analysis of 149 specimens of six species level a priori groups (*Solidago buckleyi*, *S. capulinensis*, *S. correllii*, *S. orientalis*, *S. petiolaris* and *S. wrightii*), the following six of seven traits selected in a STEPWISE analysis and used in the COMPLETE analysis are listed in order of decreasing F-to-remove values: number of mid stem leaf margin serrations (76.19), number of hairs on the disc floret ovary/fruit body (36.41), number of disc florets (15.85), involucre height (14.54), disc corolla lobe length (8.05), and disc floret pappus length at anthesis (7.21). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 2. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between *S. buckleyi* and *S. wrightii* (73.695); the smallest separation was between *S. buckleyi* and *S. orientalis* (5.774).

Table 2. Between groups F-matrix for the five a priori groups analysis (df = 6 138).

Group	buckleyi	capulinensis	correllii	orientalis	petiolaris
capulinensis	29.124				
correllii	44.705	18.173			
orientalis	5.774	14.340	18.179		
petiolaris	57.831	11.958	16.518	12.673	
wrightii	73.695	23.017	15.364	19.412	34.616

Wilks' lambda = 0.0346 df = 6 5 143; Approx. F= 24.3432 df = 30 554 prob = 0.0000

In the Classificatory Discriminant Analysis of 149 specimens of the six species level a priori groups (*Solidago buckleyi*, *S. capulinensis*, *S. correllii*, *S. orientalis*, *S. petiolaris* and *S. wrightii*) plus 1 specimen of *S. spellenbergii*, percents of correct a posterori assignment to the same a priori group ranged from 71-90%. The Classification matrix and Jackknife classification matrix are presented in Table 3. Results are presented in order of decreasing percents of correct placement. Nine of 10 specimens of the *S. capulinensis* a priori group (90%) were assigned a posteriori into the *S. capulinensis* group; 8 specimens with 96-100% probability, 1 specimen with 67% probability. One specimen of the *S. capulinensis* a priori group was assigned to *S. petiolaris* with 61% probability (37% to *S. capulinenesis*; *Lowrey 2190-B* UNM, unmounted when scored, from Mt. Capulin Nat. Mon., New Mexico). Ten of 13 specimens of the *S. correllii* a priori group (77%) were assigned a posteriori into the *S. correllii* group; 8 specimens with 98-100% probability, 1 specimen with 87% probability, and 1 specimen with 67% probability. Three specimens of the *S. correllii* a priori groups were assigned to other species: 2 specimens to *S. capulinensis* with 77% probability (10% to *S. correllii* and 9% to *S. petiolaris*; *Ward 84-028* NMC from McKittrick Canyon, Guadalupe Mts., Texas; several shoots with linear-oblanceolate basal rosette and lower to upper stem and somewhat silvery-colored leaves and with few heads) and 50% probability (45% to *S. petiolaris*; *Hershey s.n.* NMC from Guadalupe Mts., Eddy Co., New Mexico; leaves are narrowly elliptic and green); and 1 specimen to *S. wrightii* with 95% probability (*Correll 13948* LL from N. McKittrick Canyon, Guadalupe Mts, Texas; 29 cm tall shoot with persistent petiolate lower stem leaves and moderately

hairy ovaries/fruit bodies). Fifty of 66 specimens of the *S. petiolaris* a priori group (76%) were assigned a posteriori into the *S. petiolaris* group; 32 specimens with 91-95% probability (including 1 from panhandle Oklahoma and 1 from NE New Mexico), 10 specimens with 80-87% probability (including 1 from NE New Mexico), 4 specimens with 61-65% probability, and 1 specimen with 47% probability (35% to *S. capulinensis* and 17% to *S. orientalis*; *Semple & Brouillet 3753* WAT from Franklin Co., Missouri). Sixteen specimens of the *S. petiolaris* a priori group were assigned to other species: 6 specimens to *S. capulinensis* with 99% probability (*Riskind 2139* TEX from Coahuila, Mexico), 97% probability (*Wendt 545* TEX from Coahuila, Mexico), 96% probability (*Henrickson 11471* LL from Coahuila, Mexico), 84% probability (16% to *S. petiolaris*; *Ahles 35335* NCU from Calhoun Co., South Carolina), 83% probability (17% to *S petiolaris*; *Freeman 56744* NCU from Rutherford Co., North Carolina), and 73% probability (26% to *S. petiolaris*; *Semple & Heard 8268* WAT from Leflore Co., Oklahoma); 6 specimens to *S. correllii* with 92% probability (*Thomas 108653* LSU from Caldwell Co., Louisiana), 80% probability (*Thomas et al. 61516* LSU from Morehouse Co., Louisiana), 77% probability (*Thomas et al. 68478* WAT from Morehouse Co., Louisiana), 64% probability (*Thomas 137913* TEX from Ouachita Co., Louisiana), 64% probability (*Morse & Roth 8800* WAT from Chautauqua Co., Kansas), and 63% probability (*Thomas et al. 86196* WAT from Ouachita Co., Louisiana); 2 specimens to *S. wrightii* with 52% probability (40% to *S. petiolaris* and 8% to *S. correllii*; *Ahles 34674* NCU from York Co., South Carolina) and 48% probability (40% to *S. petiolaris* and 6% each to *S. capulinensis* and *S. correllii*; *Laing 575* NCU from Harnett Co., North Carolina); and 1 specimen to *S. orientalis* with 59% probability (41% to *S. buckleyi*; *Croat 1186* TEX from Douglas Co., Kansas). Twenty-seven of 36 specimens of the *S. wrightii* a priori group (75%) were assigned a posteriori into the *S. wrightii* group; 18 specimens with 90-100% probability, 6 specimens with 84-88% probability, 1 specimen with 68% probability, and 1 specimen with 54% probability (39% to *S. petiolaris*; *Wooton 325* NMC from Lincoln Co., New Mexico). Nine specimens of the *S. wrightii* a priori group were assigned to other species: 6 specimens to *S. petiolaris* with 88% probability (*Ellis 288* NMC from Bernalillo/Sandoval Co., New Mexico), 72% probability (*Wooton s.n.* NMC from Dona Ana Co., New Mexico), 64% probability (*Semple & B. Semple 10496* WAT from Gila Co., Arizona), 56% probability (32% to *S. petiolaris* and 11% to *S. correllii*; *Ward 9* NMC from Coconino Co., Arizona), 47% probability (45% to *S. wrightii* and 5% to *S. capulinensis*; *Spellenberg & Spellenberg 7926* NMC from Cascada de Basaeachic, Chihuahua, Mexico; upper stem leaves broadly lanceolate, ovary/fruit body moderately strigose), and 47% probability (40% to *S. wrightii* and 12% to *S. correllii*; *Hess 2334* NMC from Catron Co., New Mexico); and 3 specimens to *S. correllii* with 63% probability (27% to *S. wrightii*; *Noyes & Brant 202* WAT from Jeff Davis Co., Texas; broadly lanceolate to elliptic leaves, moderately strigose ovary/fruit body), 52% probability (48% to *S. wrightii*; *Moir & Fitzhugh 476* NMC from Soccoro Co., New Mexico), and 45% probability (44% to *S. petiolaris* and 11% to *S. wrightii*; *Todsen s.n.* NMC from Hidalgo Co., New Mexico; narrowly oblanceolate lower stem leaves, sparsely strigose ovary/fruit body). Twelve of 17 specimens of the *S. buckleyi* a priori group (71%) were assigned a posteriori into the *S. buckleyi* group; 11 specimens with 90-100% probability and 1 specimen with 71% probability. Five specimens of the *S. buckleyi* a priori group were assigned to other species: 3 specimens were assigned to *S. orientalis* with 88% probability (*Palmer 31511* NY from St. Francois Co., Missouri), 57% probability (37% to *S. petiolaris*; *Semple & Suripto 9917* WAT from Oregon Co., Missouri; shoot with broadly lanceolate acuminate lower and mid stem leaves with serrate margins and a damaged leader with a few heads in axillary clusters), and 55% probability (43% to *S. buckleyi*; *Letterman s.n.*, St. Louis Co., Missouri; shoot has broadly oblanceolate mid stem leaves with serrate margins); and 2 specimens to *S. petiolaris* with 96% probability (*Deam 63848* NY garden grown transplant from Posey Co., Indiana; lanceolate acuminate mid stem leaves with serrate margins) and 77% probability (17% to *S. orientalis*; *Semple & Suripto 9878* WAT from Union Co., Illinois; oblanceolate acuminate mid and upper stem leaves with serrate margins). Five of 7 specimens of the *S. orientalis* a priori group (71%) were assigned a posteriori into the *S. orientalis* group; 3 specimens with 96-100% probability and 2 specimens with 86% and 81% probabilities.

Two specimens of the *S. orientalis* a priori group were assigned a posteriori to *S. buckleyi* with 84% probability (*Hinton et al. 21617* TEX from Galeana, Nuevo Leon, Mexico; broadly oblanceolate to ovate leaves with serrate margins) and 57% probability (43% to *S. orientalis; Hinton et al. 27489* TEX from Purisima, Nuevo Leon, Mexico; broadly oblanceolate leaves with serrate margins). One specimen of *S. spellenbergii* (holotype: *Spellenberg & Jewell 9266* NMC from Parque Nacional de Cascada Basasearchic, Chihuahua, Mexico) was included a posteriori and assigned to *S. petiolaris* with 51% probability and to *S. orientalis* with 42% and to *S. wrightii* with 0% probability. The specimen does not look like the first two species; the inflorescence is long-branched and lax, and it has very sparsely strigose ovaries/fruit bodies.

Table 3. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of four a priori groups; a posteriori placements to groups in rows.

Group	buckleyi	capulinensis	correllii	orientalis	petiolaris	wrightii	% correct
buckleyi	12	0	0	3	2	0	71
capulinensis	0	9	0	0	1	0	90
correllii	0	2	10	0	0	1	77
orientalis	2	0	0	5	0	0	71
petiolaris	0	6	6	1	50	3	76
wrightii	0	0	3	0	6	27	75
Totals	14	17	19	9	59	31	76

Jackknifed classification matrix

Group	buckleyi	capulinensis	correllii	orientalis	petiolaris	wrightii	% correct
buckleyi	12	0	0	3	2	0	71
capulinensis	0	9	0	0	1	1	90
correllii	0	2	10	0	0	1	77
orientalis	2	0	0	5	0	0	71
petiolaris	0	7	6	1	49	3	74
wrightii	0	0	3	0	6	27	75
Totals	14	18	19	9	58	31	75

Two dimensional plots of CAN1 versus CAN3 and CAN1 versus CAN2 canonical scores for 150 specimens of *Solidago buckleyi*, *S. capulinensis*, *S. correllii*, *S. orientalis*, *S. petiolaris*, *S. spellenbergii*, and *S. wrightii* are presented in Fig. 14. Eigenvalues on the first three axes were 3.630, 1.373 and 0.655.

Four species level a priori groups taxa analysis
        The Pearson correlation matrix yielded r > |0.7| for most pairs of lower leaf traits and mid leaf traits reducing the number to be used to mid stem leaf length, width, and serrations and upper stem leaf length. Basal rosette leaves were rarely present and were not included in the discriminant analyses: basal leaf length, basal leaf petiole length, and basal leaf length from widest point to tip were all highly correlated. Lower leaves were sometimes absent and lower leaf traits were excluded from discriminant analyses.   Most floral traits were not correlated, but ray floret pappus length and disc floret pappus length were highly correlated and only the latter was included in the STEPWISE analysis.
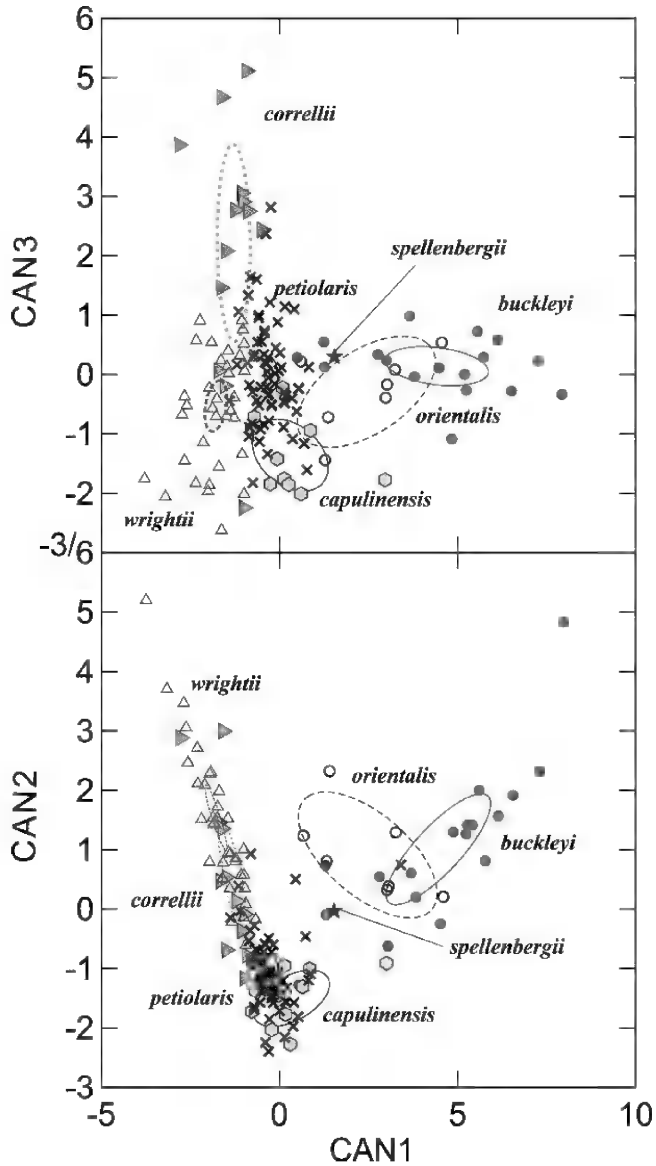
Figure 14. Plot of canonical scores (CAN1 vs CAN3 and CAN1 vs CAN2) for 146 specimens of *Solidago* subsect. *Thyrsiflorae*: *S. buckleyi* (red dots), *S. capulinensis* (pink polygons), *S. correllii* (gray right-oriented triangles), *S. orientalis* (unfilled black circles), *S. petiolaris* (black ×s), *S. spellenbergii* (green stars; a posteriori) and *S. wrightii* (unfilled blue triangles).

In the COMPLETE discriminant analysis of 125 specimens of four species level a priori groups in (*Solidago capulinensis*, *S. correllii*, *S. petiolaris*, and *S. wrightii*), the following eight traits that had the highest F-to-remove values from the nine traits selected in a STEPWISE analysis were used in the COMPLETE analysis and are listed in order of decreasing F-to-remove values: number of disc floret ovary/fruit body hairs (51.86), number of disc florets (14.58), involucre height (11.69), upper stem leaf length (8.74), disc floret pappus length at anthesis (8.73), disc corolla lobe length (5.75), number of mid stem leaf margin serrations (4.90), and number of ray florets (4.68). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 4. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between *S. petiolaris* and *S. wrightii* (24.738); the smallest separation was between *S. correllii* and *S. wrightii* (12.773).

Table 4. Between groups F-matrix for the four species level a priori groups analysis (df = 8 114).

Group	capulinensis	correllii	petiolaris
correllii	19.208		
petiolaris	14.136	14.674	
wrightii	22.089	12.773	24.738

Wilks' lambda = 0.0929 df = 8   3   121; Approx. F= 17.5043 df = 24   331   prob = 0.0000

In the Classificatory Discriminant Analysis of 125 specimens of the four species level a priori groups (*Solidago capulinensis*, *S. correllii*, *S. petiolaris* and *S. wrightii*) plus a posteriori 1 specimen each of *S. spellenbergii* and *S. wrightii* and 3 specimens of *S. correllii*, percents of correct a posterori assignment to the same a priori group ranged from 81-100%. The Classification matrix and Jackknife classification matrix are presented in Table 5. Results are presented in order of decreasing percents of correct placement. All 9 specimens of the *S. capulinensis* a priori group (100%) were assigned a posteriori into the *S. capulinensis* group; 8 specimens with 99-100% probability and 1 specimen with 81% probability. Eleven of 13 specimens of the *S. correllii* a priori group (85%) were assigned a posteriori into the *S. correllii* group; 9 specimens with 93-100% probability, 1 specimen with 87% probability, and 1 specimen with 78% probability (21% to *S. petiolaris*). Two specimens of the *S. correllii* a priori groups were assigned to other species: 1 specimen to *S. petiolaris* with 85% probability (13% to *S. wrightii*; *Hershey s.n.* NMC from Guadalupe Mts., Eddy Co., New Mexico; somewhat broader and larger mid stem leaves than most specimens of *S. correllii*); and 1 specimen to *S. wrightii* with 84% probability (*Correll 13948* LL from N. McKittrick Canyon, Guadalupe Mts, Texas; 29 cm tall shoot with persistent petiolate lower stem leaves and moderately hairy ovaries/fruit bodies). Three addition specimens of *S. correllii* were included a posteriori: one shoot of *Semple & Heard 8185* (WAT; Guadalupe Mts. N.P.) was assigned to *S. correllii* with 54% probability (37% to *S. petiolaris* and 9% to *S. wrightii*), a second shoot of *Semple & Heard 8185* (WAT) was assigned to *S. wrightii* with 97% probability, and *Carr et al. 16911* (TEX; NE tip of Bear Mt., Jeff Davis Co., Texas; leaves were narrowly lanceolate and had a slight silvery appearance to the green leaves) was assigned to *S. correllii* with 39% probability (35% to *S. wrightii* and 26% to *S. petiolaris*). Fifty-seven of 67 specimens of the *S. petiolaris* a priori group (85%) were assigned a posteriori into the *S. petiolaris* group; 48 specimens with 90-100% probability, 5 specimens with 81-89% probability, and 3 specimens with 72-77% probability. Nine specimens of the *S. petiolaris* a priori group were assigned to other species: 3 specimens to *S. capulinensis* with 100% probability (*Croat 1186* TEX from Douglas Co., Kansas), 98% probability (56 *Semple & Heard 8299* WAT from Searcy Co., Arkansas), and 53% probability (45% to *S. petiolaris*; *Riskind 2139* TEX from Coahuila, Mexico); 3 specimens to *S. correllii* with 95% probability (*Thomas et al. 86196* WAT from Ouachita Co.,

Louisiana), 87% probability (*Morse with Roth 8800 WAT* from Chautauqua Co., Kansas), and 65% probability (34% to *S. petiolaris*; *Thomas 137913* TEX from Ouachita Co., Louisiana); and 3 specimens to *S. wrightii* with 66% probability (34% to *S. petiolaris*; *Marsh 55-21 TEX* from Anderson Co., Texas), 56% probability (39% to *S. petiolaris*; *Semple 10948* WAT from Washington Co., Florida), and 55% probability (43% to *S. petiolaris*; *Ahles 34674* NCU from York Co., South Carolina). Twenty-nine of 36 specimens of the *S. wrightii* a priori group (81%) were assigned a posteriori into the *S. wrightii* group; 21 specimens with 90-100% probability, 4 specimens with 81-87% probability, 1 specimen with 62% probability, 2 specimens with 58% probability (40% to *S. petiolaris*; *Wooton 325* NMC from Lincoln Co., New Mexico) and 50% probability (47% to *S. petiolaris*; *Ward 9* NMC from Coconino Co., Arizona), and 1 specimen with 46% probability (43% to *S. petiolaris*; *Hess 2334* NMC from Catron Co., New Mexico). Seven specimens of the *S. wrightii* a priori group were assigned to other species: 4 specimens to *S. petiolaris* with 89% probability (*Ellis 288* NMC from Sandia Mts., New Mexico), 68% probability (31% to *S. wrightii*; *Wooton s.n.* NMC from Dona Ana Co., New Mexico), 63% probability (35% to *S. wrightii*; *Semple & B. Semple 10496* WAT from Gila Co., Arizona), and 51% probability (49% to *S. wrightii*; *Spellenberg & Spellenberg 7926* NMC from Cascada de Basaeachic, Chihuahua, Mexico); and 3 specimens to *S. correllii* with 91% probability (*Noyes & Brant 202* WAT from Jeff Davis Co., Texas), 66% probability (31% to *S. wrightii*; *Ward 81-582* NMC from Lincoln Co., New Mexico; leaves are broadly lanceolate to narrowly ovate), and 47% probability (39% to *S. petiolaris* and 15% to *S. wrightii*; *Todsen s.n.* NMC from Hidalgo Co., New Mexico; narrowly oblanceolate lower stem leaves, sparsely strigose ovary/fruit body). The holotype collection of *S. spellenbergii* included a posteriori was placed in *S. petiolaris* with 64% (34% to *S. capulinensis*). One collection of *S. wrightii* (*Nesom and Vorobik 5545* TEX; confluence of Rio Basaseachic and Rio Durazno Basaseachic, Chihuahua, Mexico; sparsely strigose ovaries/fruit bodies) included a posteriori was assigned to *S. petiolaris* with 78% probability (20% to S. wrightii).

Table 5. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of four a priori groups; a posteriori placements to groups in rows.

Group	*capulinensis*	*correllii*	*petiolaris*	*wrightii*	% correct
capulinensis	9	0	0	0	100
correllii	0	11	1	1	85
petiolaris	4	3	57	3	85
wrightii	0	3	4	29	81
Totals	13	17	62	33	85

Jackknifed classification matrix

Group	*capulinensis*	*correllii*	*petiolaris*	*wrightii*	% correct
capulinensis	9	0	0	0	10
correllii	0	11	1	1	85
petiolaris	4	4	56	3	84
wrightii	0	3	6	27	75
Totals	13	18	63	31	82

Two dimensional plots of CAN1 versus CAN3 and CAN1 versus CAN2 canonical scores for 127 specimens of *Solidago capulinensis*, *S. correllii*, *S. petiolaris*, *S. spellenbergii*, and *S. wrightii* are presented in Fig. 15. Eigenvalues on the first three axes were 2.106, 1.000 and 0.734.
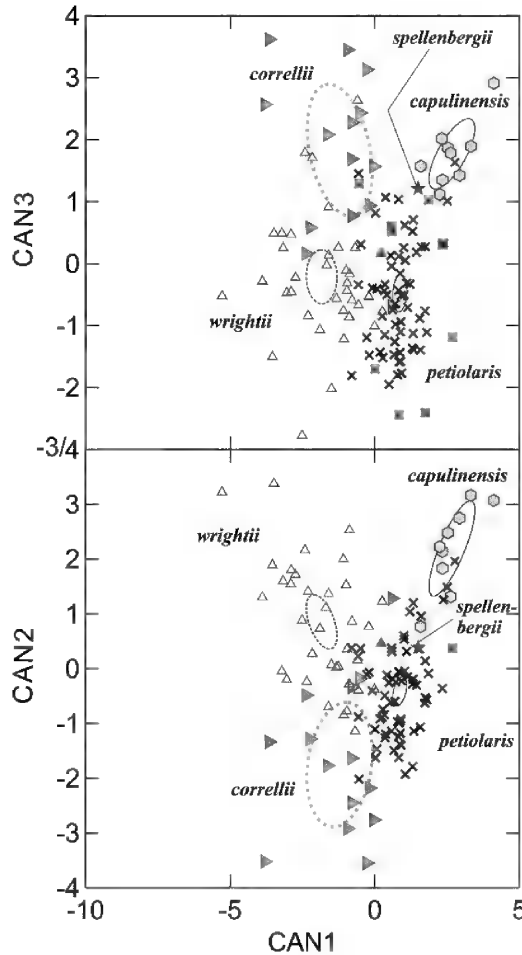
Figure 15. Plot of canonical scores (CAN1 vs CAN3 and CAN1 vs CAN2) for 127 specimens of *Solidago* subsect. *Thyrsiflorae*: *S. capulinensis* (pink polygons), *S. correllii* (gray right-oriented triangles; *Carr et al. 16911* TEX, yellow right-oriented triangles), *S. petiolaris* (black ×s), *S. spellenbergii* (green stars), and *S. wrightii* (unfilled blue triangles; *Nesom & Vorobik 5545* TEX, green-filled blue triangles).

Three varietal level a priori group analysis of S. petiolaris I

The Pearson correlation matrix yielded r > |0.7| for some pairs of leaf traits reducing the number to be used to mid stem leaf length and width and upper stem leaf width. Basal rosette leaves were always absent and could not be included. Lower leaves were often absent and lower leaf traits were excluded from discriminant analyses. Most floral traits were not highly correlated. Only ray floret pappus lengths and disc floret pappus lengths were highly correlated and only the latter were included.

In the STEPWISE discriminant analysis of 67 specimens of three varietal level a priori groups of *Solidago petiolaris* adopting Nesom's (2008) limits for groups (var. *angusta*, var. *petiolaris*, and var. *wardii*), the following seven traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: mid stem leaf width (31.93), mid stem leaf length (17.57), disc floret pappus length at anthesis (12.84), disc corolla lobe length (7.24), disc floret ovary/fruit body length at anthesis (6.74), ray floret lamina width (5.51), and disc floret corolla length (5.44). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 6. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between var. *angusta* and var. *petiolaris* (24.186); the smallest separation was between var. *petiolaris* and var. *wardii* (4.876).

Table 6. Between groups F-matrix for the three varietal level a priori groups analysis (df = 7   58); Nesom (2008) varietal limits.

Group	angusta	petiolaris
petiolaris	24.186	
wardii	8.722	4.878

Wilks' lambda = 0.1722 df = 7 2 64; Approx. F= 11.6808 df = 14 116 prob = 0.0000

In the Classificatory Discriminant Analysis of 67 specimens of the three varietal level a priori groups in *Solidago petiolaris* (adopting Nesom's 2008 limits for var. *angusta*, var. *petiolaris*, and var. *wardii*), percents of correct a posteriori assignment to the same a priori group ranged from 80-92%. The Classification matrix and Jackknife classification matrix are presented in Table 7. Results are presented in order of decreasing percents of correct placement. Twenty-two of the 24 specimens of the var. *petiolaris* a priori group (92%) were assigned a posteriori into the var. *petiolaris* group; 14 specimens with 91-100% probability, 4 specimens with 82-86% probability, 1 specimen with 78% probability, and 3 specimens with 69% probability (30% to var. *wardii*; *Radford 30382* NCU from Saluda Co., South Carolina), 67% probability (31% to var. *wardii*; *Radford 30294* NCU from Edgefield Co., South Carolina), and 63% probability (37% to var. *wardii*; *Ahles 34674* NCU from York Co., South Carolina). Two specimens of the var. *petiolaris* a priori groups were assigned to other varieties: 1 specimen to var. *angusta* with 84% probability (14% to var *petiolaris*; *Ahles 35335* NCU from Calhoun Co., South Carolina); and 1 specimen to var. *wardii* with 57% probability (43% to var. *petiolaris*; *McMillan 1993* NCU from Wake Co., North Carolina). Twenty-nine of 33 specimens of the var. *angusta* a priori group (88%) were assigned a posteriori into the var. *angusta* group; 24 specimens with 92-100% probability, 2 specimens with 88% and 84% probabilities, 2 specimens with 72% and 70% probabilities, and 1 specimen with 69% probability (19% to var. *petiolaris* and 13% to var. *wardii*; *Semple & Suripto 9936* WAT from Taney Co., Mo; non hairy phyllaries with some glands). Four specimens of the var. *angusta* a priori group were assigned to other varieties; 3 specimens to var. *wardii* with 79% probability (*Horr E573* LL from Montgomery Co., Kansas), 77% probability (Thomas et al 112964 TEX from Union Co., Louisiana) and 64% probability (22% to var. *angusta* and 14% to var. *petiolaris*; *Steward 1409* LL from Coahuila); and 1 specimen to var. *petiolaris* with 69% probability (15% each to var. *angusta* and var. *petiolaris*; *Semple & Heard 8299* WAT from Searcy Co., Arkansas; oblanceolate shiny green lower leaves to small broadly elliptic leaves above). Eight of 10 specimens of the var. *wardii* a priori group (80%) were assigned a posteriori into the var. *wardii* group; 6 specimens with 93-99% probability, 1 specimen with 79% probability, and 1 specimen with 56% probability (44% to var. *petiolaris*; *Palmer 13049* TEX from Nolan Co., Texas). Two specimens of the var. *wardii* a priori group were assigned

to var. *petiolaris* with 85% probability (15% to var. *wardii*; *Taylor & Taylor 32588* NMC from Union, New Mexico; sparsely hairy phyllaries), and 52% probability (46% to var. *wardii*; *Morse & Roth 8800* WAT from Chautauqua Co., Kansas; silvery lanceolate leaves and glandular phyllaries; this could have been assigned a priori to var. *angusta*).

Table 7. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of three varietal level a priori groups; a posteriori placements to groups in rows; Nesom (2008) variety concept.

Group	angusta	petiolaris	wardii	% correct
angusta	29	1	3	88
petiolaris	1	22	1	92
wardii	0	2	8	80
Totals	30	25	12	88

Jackknifed classification matrix

Group	angusta	petiolaris	wardii	% correct
angusta	29	1	3	88
petiolaris	1	22	1	92
wardii	0	3	7	70
Totals	30	26	11	87

A two dimensional plot of CAN1 versus CAN3 canonical scores for 67 specimens of *Solidago petiolaris* (var. *angusta,* var. *petiolaris* and var. *wardii*) are presented in Fig. 16. Eigenvalues on the first two axes were 3.009 and 0.448.
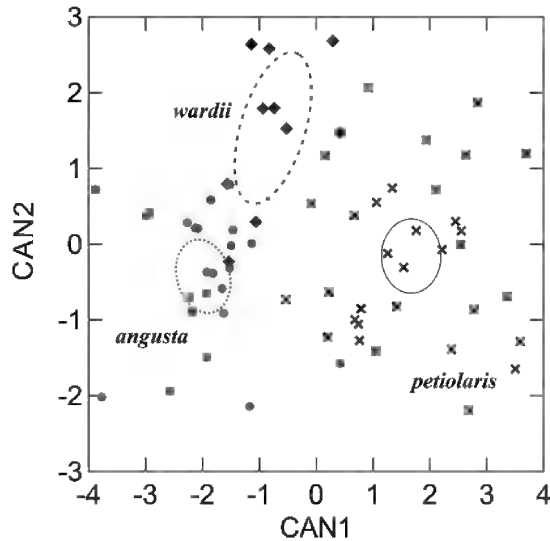

Figure 16.   Plot of canonical scores (CAN1 vs CAN2) for 67 specimens of Solidago petiolaris: var. *angusta* (green dots), var. petiolaris (black ×s), and var. wardii (black diamonds); identifications based on Nesom (2008).

Three varietal level a priori group analysis of S. petiolaris II

The same traits used in the first analysis of varieties of *Solidago petiolaris* were used except mid stem leaf width was excluded because it was used to define var. *angusta* (narrow leaves) and var. *wardii* (broader leaves). This meant that var. *wardii* extended into Missouri and Arkansas and var. *angusta* had a much more restricted distribution than shown in Fig. 13.

In the STEPWISE discriminant analysis of 67 specimens of three varietal level a priori groups of *Solidago petiolaris* (var. *angusta*, var. *petiolaris*, and var. *wardii*) adopting leaf width limits for var. *angusta* and ignoring phyllary indument features, the following three traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: disc floret pappus length (16.79), disc corolla length (14.60), and number of disc florets (8.37). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.0 00 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 8. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between var. *angusta* and var. *petiolaris* (20.919); the smallest separation was between var. *angusta* and var. *wardii* (5.545).

Table 8. Between groups F-matrix for the three varietal level a priori groups analysis (df = 3 62); alternative varietal limits.

Group	angusta	petiolaris
petiolaris	20.919	
wardii	5.545	11.756

Wilks' lambda = 0.4190 df = 3 2 64; Approx. F= 11.2619 df = 6 124 prob = 0.0000

In the Classificatory Discriminant Analysis of 67 specimens of the three varietal level a priori groups in *Solidago petiolaris* (adopting leaf width limits for var. *angusta* and ignoring phyllary indument features), percents of correct a posteriori assignment to the same a priori group ranged from 56-88%. The Classification matrix and Jackknife classification matrix are presented in Table 9. Results are presented in order of decreasing percents of correct placement. Twenty-two of the 24 specimens of the var. *petiolaris* a priori group (92%) were assigned a posteriori into the var. *petiolaris* group; 14 specimens with 91-100% probability, 4 specimens with 82-86% probability, 1 specimen with 78% probability, and 3 specimens with 69% probability (30% to var. *wardii*; *Radford 30382* NCU from Saluda Co., South Carolina), 67% probability (31% to var. *wardii*; *Radford 30294* NCU from Edgefield Co., South Carolina), and 63% probability (37% to var. *wardii*; *Ahles 34674* NCU from York Co., South Carolina). Two specimens of the var. *petiolaris* a priori groups were assigned to other varieties: 1 specimen to var. *angusta* with 84% probability (14% to var. *petiolaris*; *Ahles 35335* NCU from Calhoun Co., South Carolina); and 1 specimen to var. *wardii* with 57% probability (43% to var. *petiolaris*; *McMillan 1993* NCU from Wake Co., North Carolina). Thirteen of 18 specimens of the var. *angusta* a priori group (72%) were assigned a posteriori into the var. *angusta* group; 3 specimens with 92-99% probability, 1 specimen with 87% probability, 3 specimens with 70%-79% probability, 3 specimens with 60-69% probability, 2 specimens with 55% probability (*Thomas et al. 112964* TEX from Union Par., Louisiana) and 51% probability (46% to var. *wardii* and 9% to var. *angusta*; *Gilmore 3707* LSU from Winn Par., Louisiana), and 1 specimen with 48% probability (41% to var. *wardii* and 12% to var. *petiolaris*; *Carr 14970* LSU from Lamar Co., Texas). Five specimens of the var. *angusta* a priori group were assigned to other varieties; 4 specimens to var. *wardii* with 67% probability (17% to var. *angusta*; *Thomas & Kessler 79061* WAT from Winn Par., Louisiana), 56% probability (39% to var. *angusta*; *Miller et al. 5847* TEX from Blanco Co., Texas), 52% probability (45% to var. *angusta*; *Miller 19* TEX from Ottawa Co., Oklahoma), and 39% probability (37% to var. *angusta* and 24% to var. *petiolaris*; *Thomas 138410* LSU from Webster Par., Louisiana); and 1 specimen to var. *petiolaris* with 65% probability (31% to var. *wardii* and var.

petiolaris; *Thomas 138410* TEX from Webster Par., Louisiana). Thirteen of 25 specimens of the var. *wardii* a priori group (56%) were assigned a posteriori into the var. *wardii* group; 2 specimens with 85% probability, 1 specimen with 74% probability, 3 specimens with 60-62% probability, 4 specimens with 50-59% probability, and 1 specimen with 46% probability (32% to var. *angusta*; *Freeman 118402* TEX from Roger Mills Co., Oklahoma). Eleven specimens of the var. *wardii* a priori group were assigned to the other two varieites: 6 specimens to var. *petiolaris* with 91% probability (9% to var. *wardii*; *Taylor & Taylor 32588* NMC from Union, New Mexico; sparsely hairy phyllaries), 80% probability (18% to var. *wardii*; *Semple & Suripto 9942* WAT from Hickory Co., Missouri), 59% probability (36% var. *wardii*; *Semple & Suripto 9972* WAT from Logan Co., Arkansas; silvery leaves, non hairy resinous phyllaries), 57% probability (35% var. *wardii*; *Semple & Heard 8299* WAT from Searcy Co., Arkansas; oblanceolate shiny green lower leaves to small broadly elliptic leaves above), 47% probability (43% to var. *wardii*; *Semple & Suripto 9936* WAT from Taney Co., Mo; non hairy phyllaries with some glands), and 44% probability (34% to var. *wardii* and 22% to var. *angusta*; *Taylor 32588* LSU from Union Co., New Mexico);); and 5 specimens to var. *angusta* with 95% probability (Taylor 16926 LSU from Choctaw Co., Oklahoma; silvery narrowly ovate leaves, non-hairy resinous phyllaries), 57% probability (36% to var. *wardii*; *Semple & Heard 8268* WAT from Leflore Co., Oklahoma), 56% probability (40% var. *wardii*; *Harding 407* TEX from Delaware Co., Oklahoma), 51% probability (49% to var. *wardii*; *Riskind 2139* TEX from northern Coahuila), and 43% probability (*Morse & Roth 8800* WAT from Chautauqua Co., Kansas; silvery lanceolate leaves and glandular phyllaries; this could have been assigned a priori to var. *angusta*).

Table 9. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of three varietal level a priori groups; a posteriori placements to groups in rows; alternative variety concept.

Group	angusta	petiolaris	wardii	% correct
angusta	13	1	4	72
petiolaris	1	21	2	88
wardii	5	6	14	56
Totals	19	28	20	72

Jackknifed classification matrix

Group	angusta	petiolaris	wardii	% correct
angusta	13	1	5	67
petiolaris	1	20	3	83
wardii	5	7	13	52
Totals	18	28	21	67

A two dimensional plot of CAN1 versus CAN3 canonical scores for 67 specimens of *Solidago petiolaris* (var. *angusta,* var. *petiolaris* and var. *wardii*) are presented in Fig. 17. Eigenvalues on the first two axes were 3.009 and 0.448.

Varietal level analyses within S. wrightii

A preliminary analysis including specimens for which densities of the numbers of hairs and glands on upper stem leaves were scored was run. A plot of the number of hairs versus the number of glands on upper stem leaves is shown in Fig. 18. While specimens with no glands or no hairs could easily be assigned to var./f. *wrightii* and var./f. *adenophora* a priori groups, specimens with few to many hairs and glands could not be assigned unambiguously. More specimens had both many hairs and glands than did specimens with no hairs or no glands.
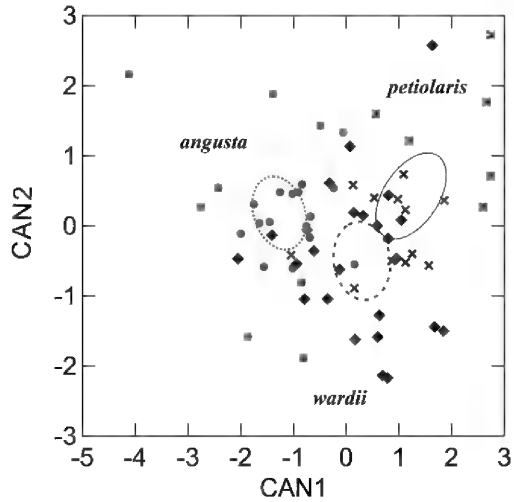
Figure 17. Plot of canonical scores (CAN1 vs CAN2) for 67 specimens of Solidago petiolaris: var. angusta (green dots), var. petiolaris (black ×s), and var. wardii (black diamnds); identification based on leaf width, phyllary hairs, and distribution.
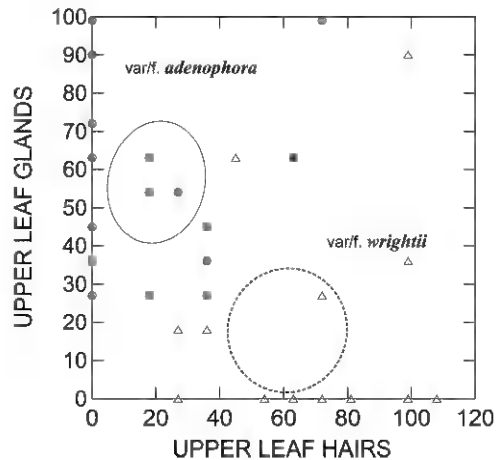
Figure 18. Plot of gland and hair numbers for 36 specimens of Solidago *wrightii*: var. *adenophora* morph (yellow dots) and var. *wrightii* morph (unfilled blue triangles); 95% confidence limits indicated by ovals; identification based on numbers of phyllary glands and hairs.

The Pearson correlation matrix yielded r > |0.7| for most pairs of leaf traits reducing the number to be used to mid and upper stem leaf lengths, mid and upper stem leaf widths, and numbers of mid of upper stem leaf serrations. Basal rosette leaves were nearly always absent and were not included in the discriminant analyses: basal leaf length, basal leaf petiole length, and basal leaf length

from widest point to tip were all highly correlated. Lower leaves were sometimes absent and lower leaf traits were excluded from discriminant analyses. Many floral traits also were highly correlated.

In the STEPWISE discriminant analysis of 36 specimens of two varietal/form level a priori groups in (*Solidago wrightii* var. *adenophora* and var. *wrightii*), the following trait was selected in a STEPWISE analysis: number of disc florets (9.48). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.0041 that the null hypothesis was true. The var. *adenophora* and var. *wrightii* had an F-to separate value of 9.483 (Wilks' lambda = 0.78192 df = 1 1 34; Approx. F= 9.483   df = 1 34   prob = 0.0041).

In the Classificatory Discriminant Analysis of 36 specimens of the two varietal level a priori groups of *Solidago wrightii* (var. *adenophora* and var. *wrightii*), the percents of correct placement a posteriori of specimens to the a priori group were 65% var. *adenophora* and 63% for var. *wrightii*. The Classification matrix and Jackknife classification matrix are presented in Table 10. Eleven of the 17 specimens of var. *adenophora* (65%) were assigned a posteriori to the var. *adenophora* group: 1 specimen with 91% probability, 1 specimen with 82% probability, 4 specimens with 72-79% probability, 4 specimens with 60-69% probability, and 1 specimen with 52% probability (*Semple & B. Semple 10496*, WAT, from Gila Co., Arizona). Six specimens of the var. *adenophora* a priori were assigned a posteriori to the var. *wrightii* group with 69% probability (*Earle 393*, NMC, from Lincoln Co., New Mexico), 59% probability (*Carter & Carter 1218*, NMC, from Catron Co., New Mexico), 59% probability (*Bye 9883*, NMC, from Mpio. Bocoyna, Chihuahua, Mexico), 56% probability (*Carter s.n.*, NMC, from Swift Trail, Graham Co., Arizona), 56% probability (Todson s.n., NMC, from Hidalgo Co., New Mexico), and 52% probability (*Metcalfe 1324,* NMC, from Sierra Co., New Mexico). Twelve of the 19 specimens of var. *wrightii* (63%) were assigned a posteriori to the var. *wrightii* group: 2 specimens with 93% and 97%% probabilities, 1 specimen with 82% probability, 2 specimens with 78% and 73% probabilities, 5 specimens with 63-69% probability, and 2 specimens with 56% probability (*Columbus 1686,* NMC, from Luna Co., New Mexico) and 52% probability (*Wooton 325,* NMC, from Lincoln Co., New Mexico). Seven specimens of the var. *wrightii* a priori group were assigned a posteriori to var. *adenophora* with 82% probability (*Van Devender 98-636,* NMC, from Mpio. Sonora, Mexico), 71% probability (*Semple & Heard 8038,* WAT, from Grant Co., New Mexico), 62% probability (*Anderson et al. 921*, NMC, from Graham Co., Arizona), 62% probability (*Ward 81-582,* NMC, Lincoln Co., New Mexico), 52% probability (*Semple & Heard 8147,* WAT, from Lincoln Co., New Mexico), 52% probability (*Hess 2334,* NMC, from Catron Co., New Mexico), and 52% probability (*Ward & Peterson 83-070*, NMC, from Hidalgo Co., New Mexico).

Table 10. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of two varietal/form level a priori groups; a posteriori placements to groups in rows; alternative variety concept.

Group	*adenophora*	*wrightii*	% correct
adenophora	11	6	65
wrightii	7	12	63
Totals	18	18	64

Jackknife classification matrix

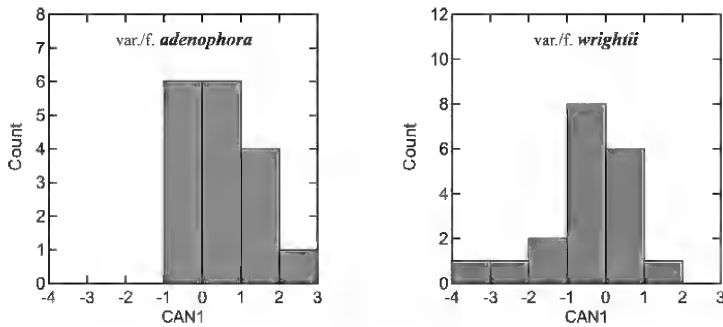| Group	*adenophora*	*wrightii*	% correct
adenophora	11	6	65
wrightii	7	12	63
Totals	18	18	64

Figure 19. Histograms of CAN1 scores for 36 specimens of *Solidago wrightii*: var./f. *adenophora* morphs and var./f. *wrightii* morphs (black diamonds); identifications based on numbers of phyllary glands and hairs.

Frequencies of CAN1 canonical scores for 36 specimens of var. *adenophora* and var. *wrightii* are presented in histograms in Fig. 19. The Eigenvalue on the first axis was 0.279.

DISCUSSION

The results from all the discriminant analyses support the recognition the following taxa in the *Solidago* subsect. *Thyrsiflorae*: *S. buckleyi*, *S. capulinensis*, *S. correllii*, *S. petiolaris* (var. *angusta*, var. *petiolaris*, and var. *wardii*), *S. orientalis*, *S. spellenbergii*, and *S. wrightii* (no varieties or forms recognized). However, not all *a priori* groups separated strongly and the percentages of specimens assigned *a posteriori* to their corresponding *a priori* groups varied and the assignment probabilities were not consistently high. Overall, the seven species are likely closely related and have not evolutionarily diverged greatly in multiple characters.

Of the two new species *Solidago correllii* and *S. spellenbergii*, (Semple 2017a and b) support was strong for recognizing *S. correllii* as a species and not just as var. *guadalupensis* in *S. wrightii*. There were similarities more frequently between *S. correllii* and *S. petiolaris* than to *S. wrightii*. Of note, one collection (*Carr et al. 16911*, TEX) annotated as *S.* aff. *correllii* (assigned a posteriori to *S. correllii* with 39% probability, 35% probability to *S. wrightii* and 26% to *S. petiolaris*) came from Jeff Davis Co., Texas and was the only specimen from that county not identified as *S. wrightii*. All other collections of *S. correllii* seen as part of this study came from the Guadalupe Mts. of Eddy Co., New Mexico, and Culberson Co., Texas, ca 80-100 mi NNW of the Jeff Davis Co. location. Although the one specimen of *S. wrightii* from Jeff Davis Co. (*Sherman et al. 202* WAT) included in the study was assigned a posteriori in the first and second analyses to *S. correllii*, it had broadly lanceolate to narrowly ovate green leaves and did not look like specimens of *S. correllii*, but the specimen had 18-24 disc florets, which is more typical of *S. correllii*, with a mean of 25 disc florets than typical of *S. wrightii* with a mean of 15 disc florets. With its elliptic-narrowly ovate leaves, *Sherman et al. 202* (WAT) was clearly not *S. correllii*, even if some floral traits were atypical.

The leaves of some specimens of *S. correllii* and some plants of *S. petiolaris* var. *angusta* were silvery from some viewing angles, but could look greener when viewed from directly above. In the field, silvery leaves of plants of var. angusta tended to be silvery and much lighter in color than other individuals of var. angusta. Thus, the silvery color is the result of light being reflected off the shiny leave surfaces (both abaxial and adaxial faces). The term "silvery" has to be used with caution because it is dependent upon the angle at which light is observed coming off leaves and because it has

been sometimes used to describe densely hairy leaves that are reflecting light of the surfaces of the hairs rather the leaf epidermis.

The sample size of N=1 for *Solidago spellenbergii* meant it could not be treated in the analyses as a separate a priori group. The a posteriori assignments of the holotype of *S. spellenbergii* to *S. petiolaris* with 51% in the first analysis and 64% in the second analysis and to *S. wrightii* with 0% and 1% certainly indicate that the holotype is not just an atypical form of *S. wrightii*, which is the only other species of subsect. *Thyrsiflorae* present in the Sierra Madre Occidental of Mexico. Four collections that were treated as *S. wrightii* and were from the Basaseachic area of Chihuahua and adjacent Sonora were included in the analyses and these were placed a posteriori into either *S. wrightii* or *S. petiolaris* (and less so to *S. wrightii*); none of these were as tall as the holotype of *S. spellenbergii* and none had mid and upper stem leaves like those of the holotype of *S. spellenbergii*. Semple (2017b) recommended additional sampling of the Cascada Basaseachic local area to find additional collections of *S. spellenbergii*. Additional sampling of the few mountainous areas between the Sierra Madre Oriental where *S. orientalis* occurs and the Sierra Madre Occidental might reveal additional undescribed narrowly endemic taxa in *S.* subsect. *Thyrsiflorae*.

In our first analysis, *Solidago buckley* and *S. orientalis* were found to be rather similar. In reality, this is not the case because there are a big differences in lower stem leaf size and shape; *S. buckleyi* has much bigger lower stem leaves than those seen of *S. orientalis*. In fact, the largest leaves in the subsection are the lower stem leaves of some *S. buckleyi* individuals. As well, *S. buckleyi* grows in the northeastern Ozarks and eastward, while *S. orientalis* is native to the Sierra Madre Oriental of mostly Nuevo Leon, Mexico (Fig. 13). In the analyses, the similarities between *S. buckleyi* and *S. orientalis* are the result of mid stem leaf serrations being selected in the STEPWISE analysis portion of the first analysis. These are the two species that consistently had obviously serrate lower and mid stem leaves. Rarely, lower and mid stem leaves of *S. petiolaris* var. *petiolaris* can be serrate but the teeth are generally smaller than those of *S. buckleyi*.

The results indicate that *Solidago petiolaris* and *S. wrightii* differ in a number of technical traits with numbers of hairs on the disc floret ovary/fruit body being significant. All specimens of *S. wrightii* had some hairs on disc floret ovaries/fruit bodies. Two-thirds of the *S. petiolaris* specimens had no hairs on the disc floret ovaries/fruit bodies, but a third did but mostly in very low numbers on the distal portions of some fruits and no hairs on others. Six collections of *S. petiolaris* included in the analyses did have sparsely to moderately hairy fruits and five of these were var. *petiolaris* plants from South Carolina, Georgia, Alabama and eastern Texas; some of these were placed a posteriori into *S. petiolaris* in the first two analyses, and some into *S. correllii* and *S. wrightii*. One plant of var. *wardii* from Kansas had sparsely strigose disc floret ovaries/fruit bodies. The ranges of the two species are essentially allopatric but are potentially sympatric in northeastern New Mexico and adjacent Colorado. It is highly unlikely that a plant with moderately hairy fruits found growing in the Carolinas, Georgia, Alabama, or eastern Texas in the Eastern deciduous woods would be a disjunct *S. wrightii*. The *S. petiolaris* plant with the hairiest fruit include the analyses came from eastern Texas and had the characteristic elongated narrow inflorescence and hairy phyllaries of var. *petiolaris*.

The two analyses of the three varieties within *Solidago petiolaris* clearly show that delineation and distribution of var. *angusta* and var. *wardii* presented by Nesom (2008) is a reasonable solution to dealing with the problem of defining the two western varieties of the species. Our results are in full agree with Nesom's observation that leaf features and phyllary features are not correlated. Presumably var. *angusta* was originally designated as a separate species on the basis of its narrow leaves and nearly glabrous phyllaries, while var. *wardii* was designated as a separate species on the basis of its silver leaf color (light reflecting off hairs?) and its canescent phyllaries. The confusion regarding the applications of the names to silver leaved specimens (either broad or narrow

leaves) and glandular or resinous non-hairy phyllaries is understandable in places like eastern Oklahoma, western Arkansas and much of Missouri where the majority of specimens do not match either the type of *S. angusta* or the type of *S. angusta*. However, by defining var. *angusta* on the basis of phyllary vestiture and accepting both green or silver, narrow lanceolate leaved morphs and green or silver ovate-leaved morphs because all these morphs have phyllaries that are not hairy and are sparsely to densely resinous (due to varying numbers of small glands), the confusion is for the most part eliminated. In this case, the silvery color is due to light reflecting of the shiny non-hairy leaf surfaces. Either a more broadly defined var. *angusta* (see the first varietal level analysis of *S. petiolaris*) or a more broadly defined var. *wardii* (see the second varietal level analysis of *S. petiolaris*) was needed. Our results indicate that the first alternative of a broadly defined var. *angusta* is much more strongly supported statistically than the latter alternative.

Support for dividing *Solidago wrightii* into a hairy var. *wrightii* and a glandular var. *adenophora* is low for both the percents of correct placement a posteriori and in the low probabilities for the correct placements. While the null hypothesis was not rejected statistically, there was no obvious way of separating plants with glandular upper leaves and phyllaries and those with hairy upper leaves and phyllaries, except by group centroid thinking, that is, forcing all specimens into one or the other group. Both the numbers of glands and the numbers of hairs were continua of variation that could not be split in a non-arbitrary way into distinct groups. In our sample, more specimens had both hairs and glands that did those with just glands or just hairs. While admittedly, the most glandular non-hairy plants are very distinct from the most hairy non-gland/minimally glandular plants, the details reveal that such plants are just the ends of continua.   Nesom (2008) opted to reduce the rank of the two varieties to just forms. Our conclusion is that even this is not justified and var. *adenophora* belongs in synonymy under the species name *S. wrightii*.

In conclusion, the seven species of *Solidago* subsect. *Thyrsiflorae* are clearly closely related but differ sufficiently in obvious and some technical traits that identification of most specimens to species should not be a great challenge when geography is also considered. Most significant is the general lack of data on basal rosette leaves. Unlike some groups of goldenrods, basal rosettes are not obvious and generally not present in the field at the time of flowering. If they were, then many more collections would include rosettes. The vast majority of specimens have no basal rosette leaves and often lacked most lower stem leaves at the time of flowering. One collection (*Wooton s.n.*, NMC) included in the study did have a well developed basal rosette and lower stem leaves and these are illustrated in Figs. 20 A-B. A second collection of *S. wrightii* (*Powell & Flyr 1493*, TEX) seen but not included in the analyses had several young rosettes present on the rootstooks; the rosette leaves were similar to those of *S. correllii* (Semple 2017a, Fig 5), but the mid and upper stem leaves were like those of *S. wrightii* and not narrowly lanceolate. The presence or absence of rosette leaves has been used in keys to identification (Semple & Cook 2006). The basal leaves in Fig. 20 are rather typical of those occurring in the genus *Solidago*, larger than some and smaller than others but possessing the winged petiolate proximal portion.

Fig. 20. Basal rosette and lower stem leaf (B) of *Solidago wrightii.* **A-B.** *Wooton s.n.* (NMC) from Dona Ana Co., New Mexico. **C.** *Powell & Flyr 1493* (TEX) from Jeff Davis Co., Texas. Scale bars = 1 cm.

Key to taxa in *Solidago* subsect. *Thrysiflorae*

1. Lower and mid cauline leaves thin, 25-50 mm wide, usually sharply or coarsely toothed, weakly to strongly acuminate, not resinous; phyllaries very sparsely stipitate-glandular; s Indiana to southern Missouri and adjacent Arkansas, disjunct in north-central Alabama .... **Solidago buckleyi**
1. Lower and mid cauline leaves firm, thick, 5-30 mm wide, rarely coarsely toothed (proximal cauline leaves may be toothed), sometimes resinous and/or stipitate-glandular; phyllaries often moderately stipitate-glandular; SE and SW USA, Mexico.

> 2. Basal rosette and lower stem leaves narrowly oblanceolate, petioles 1-4 cm long; mid and upper stem leaves lanceolate-elliptic to linear lanceolate-elliptic; phyllaries resinous, glabrate; cypselae sparsely strigose; Guadalupe Mts. in New Mexico and Texas .... **Solidago correllii**
> 2. Basal rosettes nearly always absent, lower stem leaves winged petiolate; mid and upper stem leaves narrowly to broadly elliptic; phyllaries glandular, resinous or strigose; cypselae glabrous to moderately densely strigose

>> 3. Cauline leaves serrate, proximal oblanceolate, distal oblanceolate to elliptic; cypselae moderately to moderately densely strigose; Sierra Madre Oriental, mostly Nuevo León, Mexico ....**Solidago orientalis**
>> 3. Proximal cauline leaves entire to sparsely serrate (rarely serrate in *S. petiolaris*), oblanceolate to obovate; distal lanceolate to narrowly to broadly elliptic; much of the southern USA and Sierra Madre Oriental in Mexico.

>>> 4. Cypselae very sparsely to moderately densely strigose (rarely glabrate).

>>>> 5. Cypselae moderately densely strigose; arrays rounded corymbiform to paniculiform on older shoots; cypselae +/- moderately short-strigose; Arizona, New Mexico, trans-Pecos Texas, Mexico .... **Solidago wrightii**
>>>> 5. Cypselae very sparsely strigose.

>>>>> 6. Phyllaries long attenuate, outer ½ or more the length of the inner, glandular, resinous; cauline leaves green, resinous glandular, glabrate to very sparsely strigose;

stems very sparsely sparsely villose-strigose; arrays with elongated lower branches, open; Parque Nacional de Cascada Basaseachic, Chihuahua   **Solidago spellenbergii**
6. Phyllaries lanceolate, graduated, sparsely glandular and moderately strigose distally, cauline leaves grayish-green, moderately short strigose; stems densely short villose-canescent; arrays congested narrowly paniculiform; Mt. Capulin, Union Co., New Mexico... **Solidago capulinensis**

4. Cypselae glabrous (rarely glabrate to very sparsely strigose; very rarely strigose); arrays of heads often narrow, elongated; cauline leaves entire except rarely in SE USA; SE USA to northeastern New Mexico, southeastern Colorado, Texas, northern Coahuila, Mexico
.... **Solidago petiolaris**

7. Middle and inner series phyllaries glabrous, usually minutely glandular or resinous and shiny; mid and upper stem leaves usually narrowly lanceolate, rarely broadly lanceolate to ovate, green to shiny silvery; Missouri to Louisiana west to eastern Kansas to eastern and central Texas, disjunct in northern Coahuila .... var. **angusta**
7. Middle and inner series phyllaries sparsely to moderately strigose, sometimes minutely glandular; mid and upper stem leaves lanceolate-elliptic to ovate-elliptic.

8. Involucres at anthesis 6-8 mm (mean = 7.5 mm), mid leaves 12-21(-32) mm wide; North Carolina to northern Florida west to Alabama, disjunct in east Texas
.... var. **petiolaris**
8. Involucres at anthesis 4.3-6.3(-7; mean = 5.3 mm); southern Nebraska, Kansas, western Oklahoma, western Texas, northeastern New Mexico, southeastern Colorado
.... var. **wardii**

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NEW TO OKLAHOMA: ELEOCHARIS EQUISETOIDES (CYPERACEAE)

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ABSTRACT

This paper documents an occurrence of a vascular plant species previously unreported for the flora of Oklahoma. *Eleocharis equisetoides,* a perennial spikerush, was found along a lake margin in north-central Pushmataha County.

Eleocharis equisetoides (Elliott) Torr. (Cyperaceae, subg. Limnochloa; horsetail spikerush, jointed spikesedge) is a perennial spikerush found in marshes, lakes, ponds, ditches, and streams (ITIS 2017; Smith et al. 2002). While the majority of the known populations are from coastal regions of the southeastern USA, *E. equisetoides* has also been reported as far north as Ontario (Kartesz 2014; USDA, NRCS 2017). In the USA its distribution includes Alabama, Arkansas, Connecticut, Delaware, Florida, Georgia, Illinois, Indiana, Louisiana, Maryland, Massachusetts, Michigan, Mississippi, Missouri, New Jersey, New York, North Carolina, Rhode Island, South Carolina, Tennessee, Texas, Virginia, and Wisconsin (Kartesz 2014; USDA, NRCS 2017). It is listed as critically imperiled, imperiled, or vulnerable in all but five of these states (Alabama, Florida, Louisiana, South Carolina, and Texas), and is known only historically from three (Arkansas, Massachusetts, and Missouri; NatureServe 2012). The taxon is presumed extirpated from Illinois (NatureServe 2012).

The Oklahoma collection of *Eleocharis equisetoides* (figures 1 and 2) was found at the margin of a small lake in Pushmataha County in southeastern Oklahoma. Hundreds of stems were present both in flower and fruit. Associated species included *Eleocharis obtusa, Gratiola brevifolia, Hydrolea uniflora, Rhynchospora glomerata, Utricularia radiata,* and *Zizaniopsis milacea*. The nearest populations are all over 150 miles away in Saline Co. and Union Co., Arkansas, and Anderson Co., Texas (Kartesz 2014). The nearby Lake Ninih Waiya in northern Pushmataha County and areas of the McGee Creek Reservoir in eastern Atoka County were also searched, but no additional populations of *E. equisetoides* were located. A single collection of the closely related *E. interstincta* is known from Grady Co., Oklahoma, but this is the first report of *E. equisetoides* from the state (OVPD 2017; Roalson et al. 2010; Roalson and Friar 2000).

Eleocharis equisetoides (Elliott) Torr.
Voucher specimen. **USA. Oklahoma.** Pushmataha Co.: SE of Clayton, Oklahoma, at Clayton Lake State Park, N34.54027° W95.30764°, T1N R19E Sec. 21, 19 Jul 2017, *Buthod and Hoagland AB-11596* (OKL).

Figure 1. *Eleocharis equisetoides*, natural habitat in Pushmataha Co., Oklahoma.
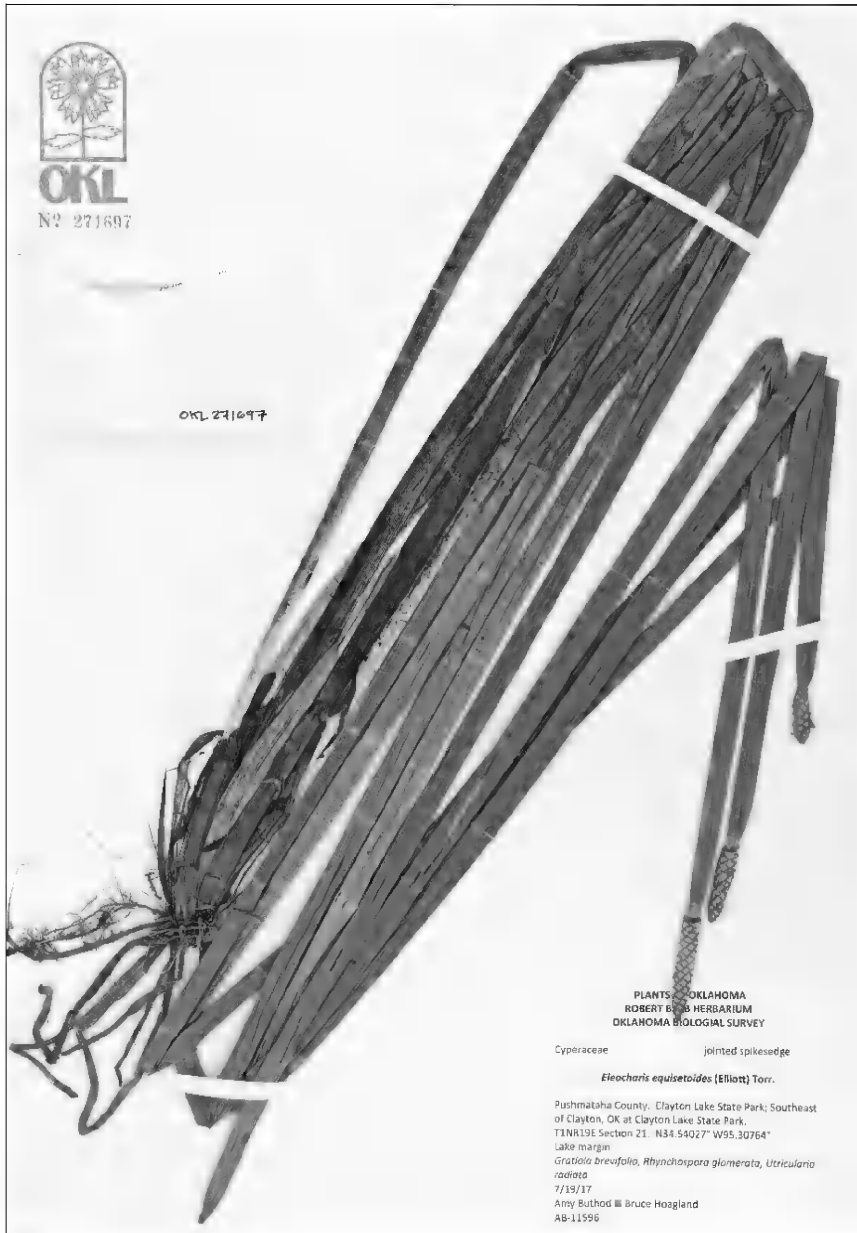
Figure 2. *Eleocharis equisetoides, Buthod & Hoagland AB11596.*

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ABELMOSCHUS ESCULENTUS AND *ALCEA ROSEA* (MALVACEAE) NEW TO THE ARKANSAS FLORA

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ABSTRACT

A*belmoschus esculentus* (L.) Moench and *Alcea rosea* L. are documented here as new to the Arkansas flora. These records also represent the first reports of these genera outside of cultivation in the state. Escaped/naturalized plants of both species were discovered growing in highly disturbed areas along the Arkansas River flood plain in Pulaski County. Additionally, *A. esculentus* is documented from Garland County on the shore of Lake Ouachita. Photographs of voucher specimens for both species are provided.

In 2007, several escaped plants of *Abelmoschus esculentus* (L.) Moench (okra) were documented from both Garland and Pulaski counties from highly disturbed habitats along the Arkansas River flood plain and the Lake Ouachita shoreline (Fig. 1). Also in 2007, escaped plants of *Alcea rosea* L. (hollyhock) were documented from Pulaski County from highly disturbed habitat along the Arkansas River flood plain (Fig. 2). No previous records of these species have been documented from the Arkansas flora, outside of cultivation (Arkansas Vascular Flora Committee 2006; Gentry et al. 2013; Bates 2015; Hill 2015).

A portion of the Two Rivers Park area consists of an expansive community garden that is a plausible source of propagules, most likely seeds from discards, compost, or abandoned plants, that could have facilitated establishment of the escaped plants. It is important to emphasize, however, that although the initial source pool is probably directly or indirectly attributable to human activities, the plants reported in this paper were escapes, and not planted, cultivated, or persisting as remnants of intentional agricultural or horticultural activities.

Abelmoschus esculentus is an annual species that is native to tropical Asia and Africa and is the okra of commerce grown both locally and commercially in the USA and elsewhere (Bailey & Bailey 1976; Bates 2015; Hanes 2015). *Alcea rosea* is a biennial species that is thought to have originated in southwestern China, but is now found in cultivation and naturalized throughout much of the world (Hill 2015). Both species are frequently cultivated in the eastern USA (Bailey & Bailey 1976; Bates 2015; Hill 2015; Weakley 2015), including Arkansas, and have been well–documented outside of cultivation in several states (Bates 2015; Weakley 2015; USDA, NRCS 2017).

Escaped/naturalized plants of these species typically are encountered in highly disturbed areas and waste places (Bates 2015; Hill 2015), similar to the environments in which the Arkansas plants were discovered. Based on frequency of cultivation and ability to self–seed, both *A. esculentus* and *A. rosea* should be expected as adventive or escaped elsewhere in Arkansas in low quality, highly disturbed environments, particularly in urban areas in proximity to where plants of these species occur in cultivation.

Alcea rosea is grown as an ornamental for its large, showy, and variously colored flowers, and *A. esculentus* is grown both as an ornamental for its showy flowers and foliage, and more commonly, for its edible fruits (Bailey & Bailey 1976).

Figure 1. A–B. Voucher specimens of escaped *Abelmoschus esculentus* from Garland and Pulaski counties. A. Specimen from Pulaski County. B. Specimen from Garland County.

Voucher specimens, *Abelmoschus*. Arkansas. Garland Co.: About a dozen plants growing on dredged spoils of recreational use area swimming beach, escaped, Brady Mt., Lake Ouachita State Park, 29 Jul 2007, *Peck 07-1745* (HEND). Pulaski Co.: One to two dozen plants growing in disturbed, sandy soils of Arkansas River flood plain, escaped, Two Rivers Park, Little Rock, 28 Jul 2007, *Peck 07-1732* (HEND); one to two dozen plants growing in disturbed, sandy soils near picnic area, escaped, Two Rivers Park, Little Rock, 29 Jul 2007, *Peck 07-1746* (HEND).

Voucher specimen, *Alcea*. Arkansas. Pulaski Co.: Seven plants growing in sandy soils of Arkansas River flood plain in oak and *Acer negundo* woods, escaped, Two Rivers Park, Little Rock, 28 Jul 2007, *Peck 07-1737* (HEND).

Figure 2. Voucher specimen of escaped *Alcea rosea* from Pulaski County.

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EUONYMUS JAPONICUS (CELASTRACEAE) NEW TO THE ARKANSAS FLORA

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ABSTRACT

Euonymus japonicus Thunb. is reported here as new to the Arkansas flora. This is the first definitive record of this species outside of cultivation in Arkansas. One spontaneous plant of *E. japonicus* was discovered growing at the edge of disturbed, urban woods in Clark County. Photographs of the plant in habitat are provided.

In 2017, a single, spontaneous/escaped plant of *Euonymus japonicus* Thunb. (Japanese spindle tree) was documented at the edge of a large expanse of highly disturbed, urban woods in Clark County (Figs. 1–2). The site, although large, is surrounded mostly by residential areas, with Rose Hill Cemetery about one block northeast of the location. No cultivated plants of *E. japonicus* were in the immediate vicinity, but a large, cultivated plant of *E. japonicus* is present in the Rose Hill Cemetery. Bird–mediated dispersal of seeds from the cultivated plant *of E. japonicus* is the presumed source of the spontaneous *E. japonicus* individual. Escaped *E. japonicus* should be expected elsewhere in Arkansas, particularly in the vicinity of where plants of the species are cultivated.

Euonymus japonicus is a large, evergreen shrub or small tree to 5 meters tall, or sometimes more, that is native to Japan (Bailey & Bailey 1976; Krüssmann 1977; Ma & Funston 2008). This species is grown in the southern USA, including Arkansas, as an ornamental for its glossy, tightly–clustered, evergreen foliage and ease of cultivation. *Euonymus japonicus* has been reported previously as a component of the naturalized floras of a few eastern states (Diamond 2013; Hannick et al. 2013; Kartesz 2015; Weakley 2015; USDA, NRCS 2017).

Voucher specimen. **Arkansas.** Clark Co.: One spontaneous/escaped plant growing at edge of highly disturbed, urban woods, off 12th St., about one block SW of the intersection of 12th St. and Main St., Arkadelphia, 29 Sep 2017, *Serviss 8600* (HEND).

Figure 1. Spontaneous plant of *Euonymus japonicus* in disturbed, urban woods in Clark County, Arkansas (plant was ca. 1.5–2 m tall). A plant of *Ligustrum sinense* (Chinese privet) also may be seen in the photo.

Three species of non–native *Euonymus* currently are known from the Arkansas flora. In Arkansas, *E. japonicus* is similar to some forms of *E. fortunei* (wintercreeper) and may be confused with it. Non–native *Euonymus* species in Arkansas may readily be distinguished using the following key.

1. Plants deciduous; young stems quadrangular in cross section, the angles often with corky wings .... **Euonymus alatus**
1. Plants evergreen (sometimes partially evergreen in *E. fortunei*); stems terete in cross section, not winged.

  2. Plant liana-like.. **Euonymus fortunei**
  2. Plant a shrub.

    3. Growth form with branches procumbent, sprawling, or ascending .... **Euonymus fortunei**
    3. Growth form erect ....**Euonymus japonicus**

Figure 2. Close–up photographs of leaves and stems of the spontaneous *Euonymus japonicus* plant.

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LYCORIS SQUAMIGERA (AMARYLLIDACEAE) NEW TO THE ARKANSAS FLORA

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ABSTRACT
Lycoris squamigera Maxim., a native of Asia, is reported here as naturalized in the Arkansas flora. About 16 naturalized plants of *L. squamigera* are reported from Garland and Pulaski counties, growing in highly disturbed habitats. Photographs of both species of *Lycoris* that occur in the state's flora, including voucher specimens of *L. squamigera*, and notes on the genus *Lycoris* in Arkansas, are provided.

In 2006 and 2007, two naturalized occurrences of *Lycoris squamigera* Maxim. (resurrection lily) were documented from highly disturbed habitats in Garland and Pulaski counties (Fig. 1). No apparent evidence of cultivation was observed, and no home sites were in the vicinity of the naturalized plants. The discovery of *L. squamigera* adds a second species of *Lycoris* to the state's naturalized flora, as *L. radiata* (L'Hér) Herb. (surprise lily, red spider lily) previously has been documented from the state (Gentry et al. 2013). *Lycoris squamigera* is a bulbaceous perennial native to China, possibly also Japan and Korea (Bailey & Bailey 1976; Hsu et al. 1994; Ji & Meerow 2000; Fig. 2). This species is grown in the southern USA, including Arkansas, as an ornamental for its large, showy, fragrant flowers and ease of cultivation. *Lycoris squamigera* has been reported previously as a component of the naturalized floras of Alabama, Ohio, and Tennessee, thus our records from Arkansas apparently represent only the fourth documented occurrence of this species outside of cultivation in the USA (Kartesz 2015; Keener et al. 2017; USDA, NRCS 2017).

Voucher specimens. **Arkansas.** Garland Co.: About a dozen plants growing in disturbed pine–oak forest on ridge and valley, 4 mi S of Lonsdale and 6 mi N of Magnet Cove, edge of county, N side of Spanish Mountain, T2S R17W S34, 3 Mar 2007, *Peck 07-103* (HEND); about a dozen plants growing in disturbed pine–oak forest on ridge and valley, plants in flower, 4 mi S of Lonsdale and 6 mi N of Magnet Cove, edge of county, N side of Spanish Mountain, T2S R17W S34, 5 Aug 2006, *Peck 06-071* (HEND). Pulaski Co.: Four plants growing on dry slope along ARK 10, W of Little Rock, S of Lake Maumelle, T3N R19W S36, 21 Apr 2007, *Peck 07-352* (HEND).

The two species of *Lycoris* present in the Arkansas flora may reliably be distinguished with the following key.

1. Perianth segments red; leaves less than 1 cm wide .... **Lycoris radiata**
1. Perianth segments pale pink to lavender–pink, the tips of the segments often tinged with lavender or purple coloration; leaves 1.5 cm wide or wider .... **Lycoris squamigera**

Figure 1. A–B. Specimens of naturalized plants of *Lycoris squamigera* from Garland and Pulaski counties. A. Specimen from Pulaski County. B. Specimen from Garland County.

Figure 2. *Lycoris squamigera*. A. Leaves. B. Scapose inflorescences – notice no leaves are present during flowering. Leaves are produced during late winter and spring, followed by flowers in mid to late summer after leaf senescence. C. Close–up view of flower.

Both species of *Lycoris* are relatively common in cultivation in Arkansas; however, *L. radiata*, a bulbaceous perennial native to China, Japan, Korea, and Nepal (Hsu et al. 1994; Ji & Meerow 2000), is more frequently encountered as naturalized and persisting from cultivation in the state (Figs. 3–4). At present, it has been documented from three Arkansas counties (Gentry et al. 2013); however, based on our observations is likely much more widespread in the state's flora than current records indicate. *Lycoris radiata* is typically observed in open, disturbed sites, waste places, fields, and lawns, but also on embankments, slopes, ravines, stream sides, and woods, where presumably water and/or gravity has facilitated dispersal of bulbs and/or possibly seeds for establishment of naturalized plants. The flowers of *L. radiata* are frequented by certain species of butterflies, such as the cloudless sulfur (*Phoebis sennae* — Fig. 5A). Plants multiply and presumably spread asexually via bulblets; however, it is unclear as to whether establishment by seed occurs in Arkansas plants. Fertile diploid and sterile triploid forms of *L. radiata* exist and are nearly identical morphologically (Hsu et al. 1994; Ji & Meerow 2000).
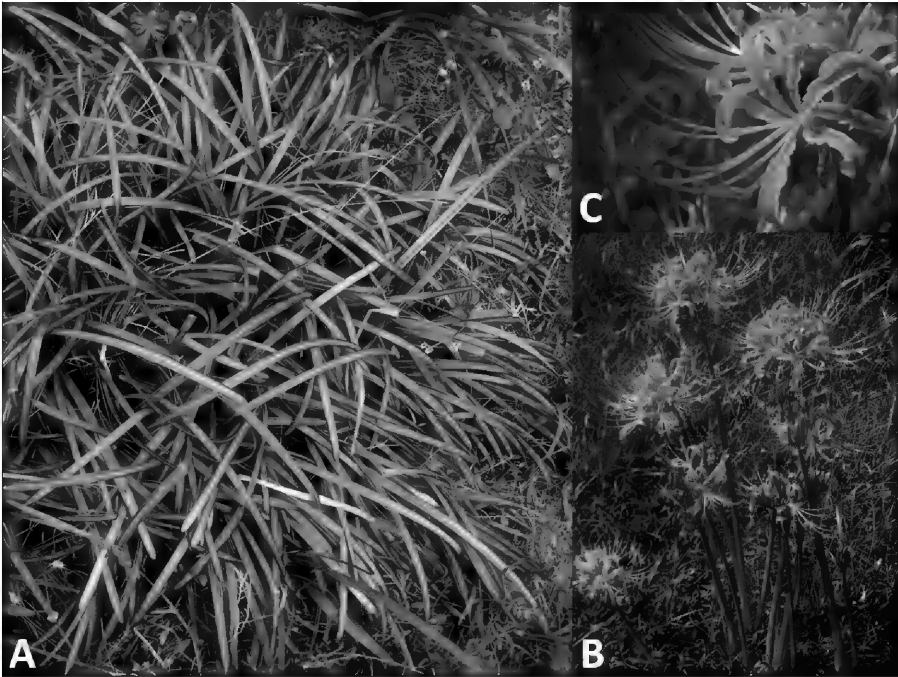
Figure 3. *Lycoris radiata.* A. Leaves. B Scapose inflorescences; the leaves in *L. radiata* follow a similar pattern to those of *L. squamigera*, with the exception of appearing soon after flowering, during mid to late autumn. C. Close–up of flower.

Figure 4. A–B. Naturalized *Lycoris radiata* in Clark Co., Arkansas. A. Plants of *L. radiata* growing on lower bank of small, intermittent stream; a portion of the streambed may be seen in the right one–third of the photograph. B. *Lycoris radiata* on a steep slope of a wooded ravine in Clark County. Several clumps of naturalized *L. radiata* plants, similar to that shown in the photograph, were present at this location.

Figure 5. A. Cultivated plants of *Lycoris radiata* in Arkansas, where two male cloudless sulfur butterflies (*Phoebis sennae*) may be seen foraging on the flowers. B. Long–persistent plant of *L. squamigera* from Hot Springs National Park in Garland County, growing at an old, remnant home site (photo credit: Brook Olsen).

In Arkansas, *L. squamigera* often is long–persistent following cultivation, which at times may give the plant the appearance of naturalization (Fig. 5B). Establishment of *L. squamigera* in Arkansas, and elsewhere, may be limited to bulblets, as apparently it is sexually sterile and possibly of interspecific hybrid origin (Kurita 1988; Hsu et al. 1994; Howard 2001), although Ji and Meerow (2000) treated it as a species, without any apparent reference to hybrid status. A combination of anthropogenic and natural processes may facilitate dispersal of bulblets, similar to the mechanisms proposed by Serviss et al. (2016) that have undoubtedly contributed to establishment of a number of sterile, hybrid taxa of *Narcissus* in the state.

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IPOMOEA BATATAS (CONVOLVULACEAE)
SPONTANEOUS IN THE ARKANSAS FLORA,
WITH ADDITIONAL NOTEWORTHY RECORDS OF ANGIOSPERMS FOR THE STATE

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ABSTRACT
Ipomoea batatas (L.) Lam. is here documented for a first occurrence in the Arkansas flora. In 2015, a single plant of *I. batatas* was discovered growing in a rubbish pile in a partially dry streambed in Clark County, Arkansas. Propagules apparently were transported by stream water from horticultural discards or cultivated plants and deposited at this site, subsequently allowing for establishment of the spontaneous plant. Additionally, in 2016 and/or 2017, six species of angiosperms: *Colocasia esculenta* (L.) Schott, *Forsythia suspensa* (Thunb.) Vahl, *Forsythia viridissima* Lindl., *Hydrangea macrophylla* (Thunb.) Ser*., Kerria japonica* (L.) DC., and *Malvaviscus arboreus* Dill. ex Cav. var. *drummondii* (Torr. ex Gray) Schery, are reported for only their second occurrences in the Arkansas flora, outside of cultivation.

In 2015, a single plant of *Ipomoea batatas* (L.) Lam. (sweet potato) was discovered growing in a rubbish pile located in the streambed of Mill Creek in Clark Co., Arkansas. Propagules apparently were transported by stream water from horticultural discards or possibly cultivated plants and deposited at this site, with subsequent establishment of the spontaneous plant (Fig. 1). This record represents the first documented occurrence of this species in Arkansas, outside of cultivation.

Ipomoea batatas is widely cultivated in the southern USA, including Arkansas, and has been documented as persistent and/or escaped from cultivation in a number of other southern states (Kartesz 2015; Weakley 2015; USDA, NRCS 2017). The species is cultivated both for horticultural purposes as an ornamental groundcover for its rapid growth and colorful foliage types, ranging from chartreuse green to reddish–purple and dark purple forms, and for its edible roots. The spontaneous plant discovered in Arkansas is one of the ornamental varieties/forms commonly planted as a ground cover.

Figure 1. Voucher specimen of spontaneous plant of *Ipomoea batatas* from Clark Co., Arkansas. Notice the adventitious roots at the top of the specimen. Establishment was likely via stem fragments that were dumped as horticultural waste and/or transported by stream water to the site, allowing for establishment of the plant.

Voucher specimen. **Arkansas**. Clark Co.: One spontaneous plant growing on rubbish heap in streambed, Mill Creek, off 26th St., immediately N of Feaster Trail parking area, Arkadelphia, 15 Oct 2015, *Serviss 8197* (HEND).

Other noteworthy angiosperm records for Arkansas

Six additional angiosperm species –– *Colocasia esculenta* (L.) Schott, *Forsythia suspensa* (Thunb.) Vahl, *Forsythia viridissima* Lindl., *Hydrangea macrophylla* (Thunb.) Ser., *Kerria japonica* (L.) DC., and *Malvaviscus arboreus* Dill. ex Cav. var. *drummondii* (Torr. and Gray) Schery –– are documented for only their second occurrences in the state, outside of cultivation.   All were documented along or within the proximity of highly disturbed, semi–wooded, urban areas in Clark and/or Garland counties. The Clark County site is a riparian zone surrounded on three sides by residential areas, with low woods immediately to the east. The stream of the main riparian zone enters and continues through the adjacent woods, where a number of non-native species, in addition to the ones cataloged in this paper, have become established. The Garland county site is at the edge of a series of old, remnant home sites, although only minor evidence of these still remains.

1. Colocasia esculenta (elephant ear, taro) is a tuberous, sometimes stoloniferous, perennial that is native to Asia, and is commonly cultivated and well–naturalized along rivers, streams, swamp margins, pond edges, drainage ditches, and bottomland hardwood forests in the southeastern USA (Godfrey & Wooten 1979; Thompson 2000; Wunderlin & Hansen 2011; Weakley 2015). Aggressive, highly stoloniferous forms of the species sometimes are referred to as *C. esculenta* var. *aquatilis* Hasskl.   *Colocasia esculenta* has been documented from Arkansas previously only from Garland County (Gentry et al. 2013). In 2017, 100s of naturalized plants of *C. esculenta* were discovered as a series of scattered individuals and colonies distributed along a highly disturbed, semi–wooded riparian zone and adjacent low woods in Clark County.

Figure 2. A–B. Naturalized plants of *Colocasia esculenta* from Clark County. Notice the elongate, several centimeter–long stolons emanating from each plant.

In the riparian zone, plants were present both in standing water of the streambed and along the banks (Figs. 2–3). Several plants also were documented at the edge of and within low woods that occurred to the east of the main riparian zone (Fig. 4). Stoloniferous offsets appeared to be the principal means of spread and naturalization.

The stolons of *C. esculenta* are extremely brittle, which allows for stolon fragmentation and subsequent transport of stoloniferous offsets by stream water, facilitating spread and establishment in the area. Many small stoloniferous offsets, such as the one shown in Figure 5, were observed.

Figure 3. Colony of naturalized *Colocasia esculenta* in streambed of riparian zone. Numerous plants, both as single individuals and small to large colonies, were present along the stream.

Figure 4. Portion of a large, expansive colony of naturalized *Colocasia esculenta* in wet woods east of the main riparian zone.

Figure 5. Presumed stoloniferous offset growing at waterline of stream. This plant was small, less than 0.5 m tall, with no other plants of *Colocasia esculenta* in the immediate vicinity.

Voucher specimen. **Arkansas**. Clark Co.: 100s of plants naturalized in and along stream of disturbed riparian zone and adjacent low woods, plants occurred both as individuals and small to large colonies, off Elaine Circle, S and E of the intersection of Elaine Circle and 21ˢᵗ St., Arkadelphia, 1 Sep 2017, *Serviss 8592* (HEND).

2. Forsythia suspensa (weeping forsythia) is a deciduous shrub to about 3 m tall that is native to China (Chang et al. 1996). It is naturalized in several states in the USA (Kartesz 2015; USDA, NRCS 2017). It was first documented outside of cultivation in Arkansas by Serviss et al. (2015). In 2016 and 2017, three additional naturalized occurrences of *F. suspensa* in Arkansas were documented from Clark and Garland counties (Fig. 6). All sites had multiple naturalized plants of *F. suspensa*. Some plants were colonial and apparently spreading vegetatively via air layering of stems. Spread via seed also is plausible, as some plants at some of the sites had fruits.

Voucher specimens. **Arkansas**. Clark Co.: Small colony of naturalized plants on bank of stream, Mill Creek, S of HSU campus, between 12ᵗʰ St. and 15ᵗʰ St., Arkadelphia, 3 Jul 2016, *Serviss 8354* (HEND); a few naturalized plants in disturbed urban woods and edge, adjacent to Pinewood Dr. and edge of HSU campus, immediately W of the Reddie Athletic Center, Arkadelphia, 17 Jun 2016, *Serviss 8350* (HEND). Garland Co.: Seven plants naturalized along small ravine, off Sleepy Valley Rd. immediately E of intersection of Sleepy Valley Rd. and Gulpha Gorge Rd., Hot Springs National Park, Hot Springs, 18 Jul 2017, *Serviss 8575* (HEND).

Figure 6. Naturalized plants of *Forsythia suspensa* growing on slope of shallow ravine in Garland County; about seven plants of *F. suspensa* were present.

3. Forsythia viridissima (greenstem forsythia) is a deciduous to semi–evergreen shrub to about 3 m tall that is native to China (Chang et al. 1996). Like *F. suspensa*, *F. viridissima* is naturalized in several states (Kartesz 2015; USDA, NRCS 2017) and was first documented outside of cultivation in Arkansas by Serviss et al. (2015). In 2017, a second naturalized occurrence of *F. viridissima* was documented from Garland County (Fig. 7). Colonies of naturalized plants of *F. viridissima* were observed from two different areas at this location. One colony consisted of nine plants established along the slope and base of a shallow ravine. The other colony consisted of numerous plants growing in and at the edge of a large thicket; this colony spanned ca. 6–7 meters across. Spread and establishment of the Garland County *F. viridissima* plants is likely a combination of vegetative air layering and also plausibly via seeds, as some plants had mature fruits.

Figure 7. Naturalized plants of *Forsythia viridissima* from Garland County. These plants occurred at the edge of disturbed woods at the bottom of a shallow ravine. Additional plants are present on a slope to the right of the area shown in the photograph. Some plants had mature fruits.

Forsythia suspensa and *F. viridissima* are morphologically similar and easily confused. For distinguishing characteristics of the two species, along with detailed photographs, see Serviss et al. (2015).

Voucher specimen. **Arkansas**. Garland Co.: Nine plants naturalized along small ravine, some plants with mature fruits, off Sleepy Valley Rd. immediately E of intersection of Sleepy Valley Rd. and Gulpha Gorge Rd., Hot Springs National Park, Hot Springs, 18 Jul 2017, *Serviss 8579* (HEND).

4. Hydrangea macrophylla (bigleaf hydrangea) is a deciduous shrub to 3 m tall that is native to Japan and commonly cultivated in the southern USA (Bailey & Bailey 1976; Krüssmann 1977; Wei & Bartholomew 2001), including Arkansas. It was first documented in the Arkansas flora by Serviss et al. (2016), which also represented only the second documented occurrence of this species outside of cultivation in the USA (Jaster et al. 2016; Serviss et al. 2016). Two additional escaped/naturalized plants of *H. macrophylla* were documented in 2017 from Clark County. Although both individuals were from the same general location, they were separated by more than 50 meters. The larger of the two plants, about 2 m tall, occurred along a small stream of a riparian zone, just above the waterline (Fig. 8).

Figure 8. Photograph of the larger of the two naturalized plants of *Hydrangea macrophylla* from Clark County. This plant was ca. 2 m tall and growing just above the water line along a small stream in a highly disturbed, semi–wooded riparian zone. Some of the lower braches were rooting via air layering, offering a potential route for localized spread and expansion.

This plant showed evidence of air layering of some of the lower branches, which were well–rooted into the soil, indicating some limited asexual spread. The second plant, which was less than 1 m tall, occurred within disturbed woods immediately east of the main riparian zone (Fig. 9). The origin of the two *Hydrangea* plants is unclear; however, horticultural discards and their potential transport via stream water to the sites of establishment is presumed.

Figure 9. Small, naturalized plant of *Hydrangea macrophylla* growing in low, wet woods immediately east of the riparian zone. Plant showed evidence of deer browse and subsequent regrowth. Its origin, although uncertain, is likely via transport of horticultural discards by water with subsequent deposition and establishment.

Voucher specimens. **Arkansas**. Clark Co.: One large plant, ca. 2 m tall, growing at edge of stream near waterline, disturbed, semi–wooded riparian zone within residential area, off Elaine Circle, S and E of the intersection of Elaine Circle and 21st St., Arkadelphia, 1 Sep 2017, *Serviss 8587A* (HEND); one small plant in disturbed, low woods, adjacent to small, intermittent stream, immediately E of Elaine Circle, Arkadelphia, 1 Sep 2017, *Serviss 8587B* (HEND).

5. Kerria japonica (Japanese kerria, Japanese yellow rose) is a deciduous shrub to 3 m tall that is native to China and Japan (Li et al. 2003; Henrickson & Weakley 2014) and is naturalized in several scattered states in the eastern USA (Henrickson & Weakley 2014; USDA, NRCS 2017). It was first documented outside of cultivation in Arkansas by Peck and Serviss (2016) from Garland County, based on a 2006 specimen (*Peck 06-046*). It is important to note that, although this second occurrence also is from Garland County, it is from a different location than the original Peck specimen and documented more than a decade later.

In 2017, naturalized plants of *K. japonica* were observed growing at the base of a slope of a shallow ravine in Hot Springs National Park. Plants appeared to be spreading via root suckers, which is typical for this species (Fig. 10). The origin of the naturalized plants may have been cultivated plants of *K. japonica*, as the location of the naturalized plants is adjacent to a series of old home sites.

Figure 10. Naturalized plants of *Kerria japonica* in Garland County, Hot Springs National Park. About 10 plants/clones were present at this location, presumably established via root suckering. To the left is the base of the ravine which may hold water intermittently. The darker colored plants more to the background (right side of photograph) are *Forsythia viridissima*, which also was naturalized at this location.

Voucher specimen. **Arkansas**. Garland Co.: About 10 plants naturalized on slope of small ravine near base, plants appearing to be spreading vegetatively via root suckers, off Sleepy Valley Rd. immediately E of intersection of Sleepy Valley Rd. and Gulpha Gorge Rd., Hot Springs National Park, Hot Springs, 18 Jul 2017, *Serviss 8580* (HEND).

6. Malvaviscus arboreus var. **drummondii** (wax mallow) is a small, evergreen shrub (semi–woody subshrub in Arkansas) to ca. 3 m tall that is native to Mexico and Texas and naturalized in a few southeastern states (Bailey & Bailey 1976; Krüssmann 1977; Diggs et al. 1999; Weakley 2015). It only has been documented previously in Arkansas from Drew County (Sundell 1986; Gentry et al. 2013). In 2017, a single, large, naturalized plant of *M. arboreus* var. *drummondii* was documented growing at the top of a stream bank in a disturbed, semi–wooded riparian zone in Clark County (Fig. 11). No other plants of *M. arboreus* var. *drummondii* were observed in the vicinity.

The mature fruits of *M. arboreus* var. *drummondii* are bright reddish–orange and presumably (the seeds) are bird–dispersed. *Malvaviscus arboreus* var. *drummondii* is occasionally cultivated in the Arkadelphia area, and bird–mediated dispersal of seeds from cultivated plants is presumably the source of the naturalized plant.

Figure 11. Naturalized plant of *Malvaviscus arboreus* var. *drummondii* in Clark County. A single plant occurred in a highly disturbed, mostly open area at the top of the stream bank, growing amidst a large population of *Chamaecrista fasciculata*.

Voucher specimen. **Arkansas**. Clark Co.: One plant growing on top of stream bank in open area of disturbed riparian zone, plant with flowers, off Elaine Circle, S and E of the intersection of Elaine Circle and 21st St., Arkadelphia, 1 Sep 2017, *Serviss 8585* (HEND).

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ECOLOGY OF AN ENDANGERED *GENTIANA FLAVIDA* POPULATION IN EAST-CENTRAL KENTUCKY

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ABSTRACT

An ecological study of a population of the Kentucky-endangered *Gentiana flavida* was conducted in a 0.11 ha (1100 m^2) macroplot in Madison Co., Kentucky. Cream gentians occur in a mesic prairie inclusion meadow and mixed hardwood-red cedar forest edge on a southwest-trending rocky lower slope. They occur in low foliage coverage (8%) and do not thrive well under total shade compared to partial shade or full sun. The population is threatened by exotic invasive taxa (mainly the grasses *Arthraxon*, *Microstegium*, and *Schedonorus*), encroachment of woody plants from the forest edge, and potential herbicide-spraying along a powerline corridor that passes through the macroplot. In a floristic survey of the macroplot, 211 vascular plants species (192 native, 19 non-native) in 156 genera were recorded; 143 species were identified in 30 (1 m^2) quadrats; 68 species in the macroplot did not appear in quadrats. Sixteen of the 19 exotic naturalized taxa are state-listed invasives.

We studied aspects of the biology and ecology of a population of *Gentiana flavida* A. Gray (cream gentian) in southeastern Madison Co., Kentucky, within the Eastern Knobs Region of the Western Alleghany Plateau (Figure 1). The cream gentian is an endangered species in Kentucky, observed only in five counties from wet calcareous prairies and open woodlands (KSNPC 2017). The present overall distribution is restricted to small isolated populations in 13 Midwestern states and one extant population in Ontario, Canada (Pringle 2017; Figure 2).

The 0.11 ha (1100 m^2) Madison County macroplot is rectangular-shaped and situated on private land from 243 to 248 m elevation above sea level at latitude 37.60273° N and longitude 84.15260° W (Figure 1). Our study was made from August 2013 to October 2014 and from April to September 2017. Jean's Glade, the study site, is named to honor the memory of Jean Horrar, the landowner who initially preserved the gentian population. The present article provides the first descriptive ecological and floristic study for a Kentucky cream gentian population.

Morphology and phenology

Gentiana flavida is a glabrous, native perennial forb from 40 to 95 cm tall from a stout unbranched stem and a long, thick taproot (Pringle 1963, 1965, 1967; Wood & Weaver 1982). Plants produce 1–10 erect ramets with a laxly erect to sprawling habit, where several mature stems arise from older rootstocks (Pringle 1965; Figures 3, 4, 5, 6). In Kentucky, flowering begins in early August through October and concludes with seed dispersal from capsule dehiscence in late October– early November. Pollination is effected by bumblebees (*Bombus* spp.).

Taxonomy

      Gentiana flavida is one of 13 *Gentiana* species in sect. Pneumonanthae, tribe Gentianeae, family Gentianaceae, within eastern North America (Pringle 1967) and one of 27 *Gentiana* species treated in the *Flora of North America North of Mexico* (Pringle 2017). The correct scientific name of the cream gentian has been of considerable debate (Pringle 1963, 1965, 1967, 2017; Wilbur 1988; Gandhi, Greuter, & Wiersema, pers. comm. 2017). Muhlenberg (1813) named the cream gentian (*Gentiana alba* Muhl.) but did not provide a description (Wilbur 1988; Gandhi, Greuter, & Wiersema, pers. comm. 2017). The name *G. alba* Muhl. ex Nutt. has often been cited, but Nuttall (1818) but gave no validating information beyond Muhlenberg. Gray (in Gray & Sullivant 1846) validly named the cream gentian as *G. flavida* A. Gray.

      Several common names have been used for *Gentiana flavida*, largely based on various flower colors: white gentian, white plains gentian, white prairie gentian, pale cream gentian, pale gentian, plains gentian, yellowish gentian, and yellow gentian (Waldron 2001; Heikens 2002; Bowles & Jacobs 2010; Bebeau 2014; Pringle 2017).

Geographic distribution

      Gentiana flavida is native to eastern North America in the midwestern and eastern USA and Ontario, Canada (Pringle 1963, 1967, 2017; Kartesz 2015; NatureServe 2017; Figure 2). Cream gentian populations are imperiled throughout much of their distribution range because of extreme habitat losses primarily from anthropogenic disturbances, forest expansion, absence of fire, and invasive grasses and forbs. The overall decline of eastern populations has been affirmed, and the continued existence of peripheral populations surviving as isolated prairie remnants has significantly decreased in recent years (Pringle 1963, 1967, 2017).

Figure 1. *Gentiana flavida* in Jean's Glade, among foreground mesic prairie inclusion meadow and background subxeric mixed hardwood-red cedar forest edge.
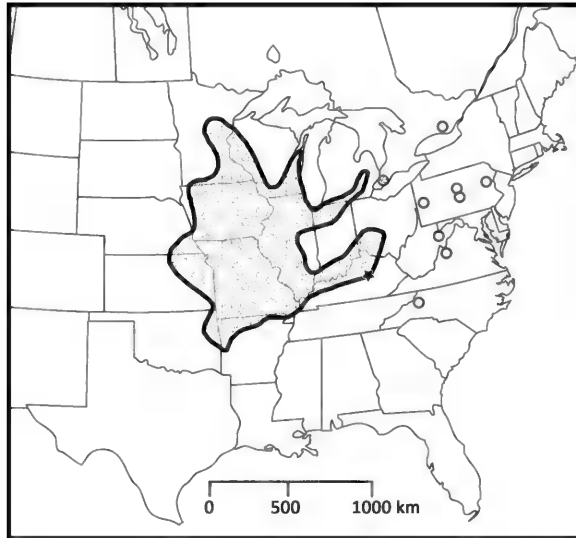
Figure 2. Present-day distribution (shaded outline) of *Gentiana flavida* in the USA and Canada and extirpated populations (hollow circles), after Pringle (1967, 2017). A disjunct relic Ontario population lies above Lake Erie and below Lake Huron. A star symbol marks the Madison County site in east-central Kentucky.

Figure 3. *Gentiana flavida* genet with several unbranched, sprawling ramets in the mesic prairie inclusion meadow.

Figure 4. *Gentiana flavida* with simple, opposite cauline and whorled terminal leaves (*Thompson 17-480*, BEREA).

Figure 5. Terminal and axillary inflorescences of *Gentiana flavida* with two brown marcescent axillary flowers (*Thompson 17-480*, BEREA)

Figure 6 *Gentiana flavida* terminal inflorescence of partially open corollas adapted to bumblebees (*Thompson 17-480*, BEREA).

Pringle (1963) inferred that the original center of populations for *Gentiana flavida* was west of the Mississippi River, possibly the Ozark Highlands, with the gentian migrating eastward with the expansion of tallgrass prairie vegetation during the post-Wisconsin xerothermic period, and that the current eastern populations are prairie relicts or prairie remnants, as evidenced by wide-ranging native tall grasslands where most extant populations are found.

The North American *Gentiana flavida* distribution (Figure 2) formerly extended from Arkansas, Oklahoma, Missouri, Kansas, Nebraska, Iowa, Minnesota, Wisconsin, Michigan, Illinois, Indiana, Kentucky, Ohio, to scattered outlier populations in Maryland, Pennsylvania, West Virginia, Virginia, North Carolina, and Ontario, Canada (Pringle 1963, 1967; NatureServe 2017; USDA, NRCS 2017). The current USA range extends from Arkansas, Oklahoma, Missouri, Kansas, Nebraska, Iowa, Minnesota, Wisconsin, Michigan, Illinois, Indiana, Ohio, and Kentucky (Pringle 1967, 2017; Figure 2). Outlier populations in North Carolina, Pennsylvania, Virginia, and West Virginia have been extirpated (Figure 2), and a Maryland report was erroneously based upon a misread specimen label from Indiana (Pringle 2017). Kartesz (2015) mapped Pennsylvania and North Carolina as extirpations. The distribution map of *G. flavida* (Figure 2) illustrates the one relic population remaining above Lake Erie in southwestern Ontario (Waldron 2001; Bowles & Jacobs 2010) and the 13 USA historic records (Pringle 1967, 2017).

Habitats

Principal habitats of the cream gentian are calcareous substrates with vegetation dominated by native warm-season prairie grasses and forbs (Pringle 1965; 2017; Heikens 2002). Pringle (1965) determined that *Gentiana flavida* is an obligate calciphile prairie species. Hilty (2008) recorded gentian habitats in Illinois from mesic prairies, sandy oak savannas, rocky bluffs, upland forest edges, and limestone glades. Calcareous gentian habitats in Missouri include rocky prairies, rocky wooded slopes, rocky open limestone and cherty limestone glades and bluff escarpments (Steyermark 1963; Yatskievych 2013). Andreas and Cooperrider (1981) reported the species in Ohio from upland mesic prairies, glades, open upland forests, prairie openings, and grassy fields. In Minnesota, Bebeau (2014) indicated that cream gentian grows in well-drained soils of moist meadows, prairies, and open woodland habitats under partial shade or full insolation. At Walpole Island, Lambton County, Ontario, the last extant Canadian population is restricted to a remnant of mesic to dry oak-hickory savannah in calcareous soils (Waldron 2001; Bowles & Jacobs 2010).

Campbell and Medley (2012) noted that cream gentian occurs in native grassland remnants, usually in damp limestone-based soils, in Kentucky. Actual documentation in the last 30 years has only been from the Eastern Knobs and the Bluegrass Regions (Campbell & Medley 2012). Although Kartesz (2015) mapped ten Kentucky counties, the Kentucky atlas by Campbell and Medley (2012), mapped only Robertson and Rowan counties from voucher specimens with non-verified reports from Butler, Lewis, Logan, Madison, Pendleton, and Warren counties. The western counties, Butler, Logan, and Warren, are doubtful without actual specimen documentation (Campbell & Medley 2012). The KSNPC (2017) reports Butler and Warren counties as historic observations and records the gentian from past observations in Lewis, Madison, Nicholas, Robertson, and Rowan counties, but without any voucher specimens.

Kentucky documentation

Prior to the population assessment at the Madison County site, actual specimen documentation has been verified from only three counties on soils derived from Ordovician limestone or Silurian limestone and dolomite in east-central Kentucky. A historic Pendleton County specimen near Falmouth was collected in September 1931 within the Hills of the Bluegrass Ecoregion (*Barton s.n.*, BEREA!, KY!). In 1985, Medley (1993) collected a cream gentian in Robertson County in a rocky limestone prairie of a cedar glade woodland at Blue Licks Battlefield State Resort Park within

the Hills of the Bluegrass Ecoregion (*Medley 13564-85*, DHL! now at APSC). A third specimen was collected on 16 September 1987 from a population on an open grassy ridgetop in limestone soil near Clearfield, Rowan County, within the Western Allegheny Plateau (*Hammer 538*, EKY!). The first Madison County collection from our study area in Silurian-derived calcareous soils was 21 August 2002, within the Knobs-Lower Scioto Dissected Plateau Ecoregion of the Western Allegheny Plateau (*Thompson 02-392*, BEREA!).

Conservation rankings

The KSNPC (2017) classifies *Gentiana flavida* for the Kentucky State Protection Status as an Endangered species. NatureServe (2017) ranks it in Kentucky as S1S2 (critically imperiled to imperiled). The species is classified a Global rank of G4 (apparently secure) and a national rank of N1 (critically imperiled). In Ontario, the single mesic oak-hickory savannah population is ranked S1 (critically imperiled), and Nationally Endangered (Waldron 2001; Bowles & Jacobs 2010). The cream gentian is listed as SH (historic) in North Carolina and Pennsylvania and S1 (critically imperiled) in Michigan, Nebraska, Oklahoma, and West Virginia, S2 (imperiled) in Indiana, Kansas, and Ohio, and S3 (vulnerable) in Iowa and Wisconsin. Arkansas, Illinois, Minnesota, and Missouri are SNR (rank not yet assessed); populations in those states are presumed secure (NatureServe 2017). Extirpated populations in North Carolina, Pennsylvania, Virginia, and West Virginia have provisional SH (historic) rank status (Pringle 2017; Figure 2), although these states are not all currently mapped as extirpated by Kartesz (2015), NatureServe (2017), and USDA, NRCS (2017).

THE GENTIAN STUDY SITE

Physiographic Ecoregions

The Knobs Region is a narrow horseshoe-shaped belt of rugged east and west mountain topography typically known as "Knobs." The Knobs, marked as Eastern and Western Knobs, encircle the Kentucky Outer Bluegrass Region (Burroughs 1926; Fenneman 1938). These conical knobs (erosion remnants) are numerous, flat-topped, or domed-shaped with concave upper slopes at lower elevations due to capstone Pennsylvanian escarpments remaining after easily eroded shale and siltstone have been severely cut by streams over time (Fenneman 1938; McFarlan 1943; Newell 1981; Muller & McComb 1986). The Knobs characteristically occupy narrow valleys to broad alluvial floodplains of first-order and second-order streams dissecting the nearby escarpments. A thick colluvium emerges on lower hillside slopes to form alluvial floodplains on V-shaped valleys and eventually to U-shaped valleys (Newell 1981).

Campbell (2003) mapped the physiography of the Knobs Region based on soils, geology, topography, vegetation, and biogeography. He described the Kentucky Ecoregional Sections in the vicinity of Jean's Glade, as the Knobs Region and Transitions, which are situated between the Eastern Bluegrass to the west and the Black Shale-Siltstone Knobs of the Appalachian Plateau to the east. To be more precise, the environs with the gentian site are located within the Dolomitic Plains and Foothills and Foothill Flats and Knob Valleys Sections from Campbell (2003).

Woods et al. (2002) designated the Knobs Ecoregions as belonging to the Knobs-Lower Sciota Dissected Plateau of the Western Allegheny Plateau in the vicinity of Jean's Glade. The Western Allegheny Plateau has local relief, elevation, and forest density much greater than in the Interior Plateaus (Woods et al. 2002).

Geology

The Knobs-Lower Sciota Dissected Plateau is overlain by a mixture of capstone Pennsylvanian-age strata shale, siltstone, sandstone, and conglomerate at higher knob elevations and Silurian-age shale and dolomite at lower elevations (Peterson 1981; Noger 1988; Woods et al. 2002).

Sedimentary rock outcrops are commonly present in nearly all geologic systems of the Western Allegheny Plateau (Woods et al. 2002).

The mapped geology of the immediate surroundings of Jean's Glade is the Crab Orchard and Brassfield Dolomite Formations of the Lower and Middle Silurian System (Weir et al. 1971; Peterson 1981). The Crab Orchard Formation comprises greenish-gray clay shale and minor dolomite 12 to 18 m thick to the base. Weir et al. (1971) reported Crab Orchard shale and dolomite to be the thickest at Stillwater Branch, the second-order stream abutting Jean's Glade. This formation lies concordantly over the 3 to 6 m thick olive-green to yellowish-green dolomite of the Brassfield Dolomite Formation (Weir et al. 1971; Peterson 1981).

Soils

The general soil map unit for Madison County in the environs of Jean's Glade belongs to the Colyer-Weikert-Captina Soil Association (Newton et al. 1973). Soils of this association are shallow, poorly to moderately well drained, and occur along near level floodplains to lower hillside slopes within the Knobs Region (Newton et al. 1973). The two soils series at Jean's Glade are Newark silt loam and Shrouts silty clay loam (Newton et al. 1973; Soil Survey Staff 2017).

Newark silt loam, the principal soil series of Jean's Glade, is present on a nearly level alluvial floodplain of Stillwater Branch. Newark series on 0 to 4 percent slopes are somewhat poorly drained alluvial soils washed from limestone, shale, and siltstone; they are often flooded in the wet winter and early spring when the seasonal water table is 15 to 46 cm (Newton et al. 1973). A dark grayish-brown silt loam about 40 cm deep, Newark series is moderately permeable with high moisture capacity, very slow surface runoff, medium organic matter content, and a soil reaction pH near neutral (6.6 to 7.3) throughout the solum (Newton et al. 1973). Newark silt loam is the only soil of this series mapped in Madison County by Newton et al. (1973). At Jean's Glade, Newark silt loam is intermingled with Shrouts silty clay loam on the lower rocky slope of the *Juniperus-Quercus-Fraxinus-Ulmus-Cercis* Forest Edge.

Shrouts silty clay loam is severely eroded residuum from calcareous clay shale and brown-colored dolomite on hillsides of V-shaped valleys in the Knobs Region (Newton et al. 1973). This series consists of neutral to slightly alkaline, well-drained soils with a solum only 20 to 40 cm thick and a shallow root zone. Shrouts series occupy foot slopes from 6 to 12 percent to moderately steep 12 to 30 percent lower slopes (Newton et al. 1973). Available moisture capacity is low to very low or droughty within the root zone due to a slowly permeable clay layer. The depth to brown Silurian bedrock is 1.5 to 2.1 m with surface rock outcrops common. Vegetation with stands of *Juniperus virginiana* are characteristic of Shrouts clay series (Newton et al. 1973; Woods et al. 2002).

The neutral to mildly alkaline pH of the Newark soil series at Jean's Gentian Glade was confirmed through two separate soil sample analyses. Soil samples taken at five different locations within the glade macroplot revealed pH ranges from 6.7 to 7.4 with a mean of 7.2 (Sears 2014). An earlier pH analysis from a single Newark soil sample was a neutral-mildly alkaline 7.35. The soil texture was 21% sand, 53% silt, and 26% clay (Thom 2006). These two soil reports indicated high levels of potassium, magnesium, and calcium with low phosphorus. Thom (2006) reported the high calcium and magnesium values are related to the soil water above 7.0 pH. He stated potassium levels are most likely so high due to the large amount of dead *Juniperus virginiana* leaves on the soil surface where the nutrient readily leaches into the soil during rainfall. Thom (2006) concluded that "... the shallow soil depth indicates the present soil was formed from and remains heavily influenced by the underlying rock." This is especially relevant due to the significant number of species recorded in the macroplot that grow preferentially, or exclusively, in neutral to mildly alkaline calcareous soils.

Vegetation

The pre-settlement vegetation of the Knobs Region contained elements of the Mixed Mesophytic Forest and more so, the Western Mesophytic Forest, a transition of Oak-Hickory and Mixed Mesophytic Forest (Braun 1950). Forest resources in the Knobs Region have been utilized for lumber and charcoal since settlement in the late 1700s. Forest removal was most extensive during the period between 1808 and 1875 with only remnants of the original vegetation occupying steeper landscapes (Burroughs 1926). The distribution of species is strongly influenced by the parent material and soil/site conditions within the Knobs Region (Braun 1950, 1955). In strong contrast to the Pennsylvanian Allegheny Plateau to the east and Ordovician Bluegrass to the west, a portion of the Knobs Region is underlain by Silurian calcareous limestone strata that develop into limestone soils (Braun 1950; Peterson 1981).

Küchler (1964) described the potential vegetation in this region of Kentucky as *Quercus-Carya* Forest. The upland forested Knobs Region today predominately consist of *Quercus* and *Quercus-Pinus* vegetation. Forest vegetation on calcareous upland knob slopes includes *Quercus-Fraxinus* stands with a common *Juniperus virginiana* component (Woods et al. 2002). Muller and McComb (1986) studied eight upland forest sites in the Eastern and Western Knobs Region. They recognized Mesophytic Hardwood plots comparable to the Mixed Mesophytic Forests of the Cumberland Plateau of Braun (1950), which were readily separated from *Quercus alba*, *Q. coccinea*, and *Q. montana* plot sites. Important mesophytic hardwoods included *Acer rubrum*, *A. saccharum*, *Fagus grandifolia*, *Fraxinus americana*, *Liriodendron tulipifera*, *Quercus alba*, *Q. montana*, *Q. rubra*, and *Sassafras albidum* (Muller & McComb 1986). Jones and Thompson (1986) reported similar canopy tree composition, except for the absence of *Tsuga canadensis*, from a beech-hemlock stand in the Knobstone Escarpment (Knobs Region of Quarterman and Powell 1978) in extreme southeastern Madison County, ca. 11.0 km southeast of Jean's Glade.

In the Knobs Border Area east of the Kentucky Bluegrass section, isolated prairie inclusions (prairie relics) originally were surrounded by mesic forest types (Braun 1950, 1955). Where limestone was the underlying rock, the dominant species of the secondary forest communities were *Juniperus virginiana* and *Cercis canadensis* (Braun 1950). These relic prairie communities and scattered prairie species occurred along bands of Silurian dolomite and limestone outcrops in the Knobs Border Area (Braun 1950, 1955). Jean's Glade is an excellent example of a relict prairie inclusion habitat adjoining a subxeric mixed hardwood-red cedar forest edge.

Climate

Kentucky precipitation generally is distributed throughout the year although droughts may occur during hot, humid summers. Mildly cold winter temperatures are often are accompanied by minor snowfall (Trewartha & Horn 1980). Data from the Lexington Airport (1981–2010) report the mean annual precipitation (115 cm), lowest in January and February (8 cm), highest in May (13 cm), and a mean annual snowfall (33 cm). Mean annual temperature is $13.1°$ C with the coldest in January ($3.3°$ C) and warmest in July ($25.6°$ C). Median length of the growing season is 195 days above the base $0°$ C (MRCC 2017).

METHODS

A floristic study of vascular plants was made at Jean's Glade during August 2013 through October 2014 and April to September 2017 within a 0.11 ha (1100 m^2) measured macroplot. Thirty (1 m^2) quadrats were non-randomly placed to include the presence of a gentian genet to determine absolute frequency within the macroplot. Relative frequency, the number of quadrats with a species divided by 30 quadrats x 100 converted to a percentage, is a measure of abundance, distribution, and probability of a species' occurrence. Each taxon within the macroplot was given a locally inclusive relative abundance value following Thompson et al. (2012): R (Rare)–1 to 4 plants or genets; S

(Scarce)–5 to 10 plants or genets; I (Infrequent)–11 to 30 plants or genets; O (Occasional)–31 to 100 plants or genets; F (Frequent)–101 to 1000 plants or genets; and A (Abundant)–greater than 1000 plants or genets. Plant habitats were determined through field reconnaissance and sampling data of characteristic and dominant species in conjunction with physical site factors (geology, soils, topography, slope aspect, temperature-moisture regimes, and physiognomy). Species within the macroplot were documented with a representative voucher and deposited in the Ralph L. Thompson Berea College Herbarium (BEREA).

The percent foliar cover of 268 gentians within the macroplot was estimated visually. To determine gentian cover, 100 (1 m^2) quadrats were non-randomly placed along six transects to account for all 268 genets in the population and their respective ramets, when present.

Gentian ramets were non-randomly selected and their heights measured under three insolation conditions: full sun (mesic meadow), partial shade (near the tree line of the adjacent forest edge), and full shade (within the forest edge overstory boundary). Twenty ramets were selected for both full sun and partial shade areas. Only fifteen ramets for the full shade area were available for measurement. Non-flowering ramets were measured, using a meter stick, from the ground to the apex of the stem and an average was determined for each group. Plants were measured during the first week of August 2015, approximately one month before they began to produce flowers.

Manuals for identification or verification of taxa are Jones (2005), Tennessee Flora Committee (2015), and Weakley (2015). Nomenclature is established by the Tennessee Flora Committee (2015) except for a few taxa from USDA, NCRS (2017). Clade sections are from Weakley (2015). Non-native invasive status is determined by KY-EPPC (2013).

RESULTS AND DISCUSSION
Three major plant habitats are designated within the 0.11 ha macroplot and described with associated species in conjunction with Appendix 1 (Quadrat Frequency), Appendix 2 (Species List), and Table 1 (Taxonomic Summary). Quantitative data are examined from quadrat sampling, relative abundance, gentian foliar cover, gentian height, and a floristic summary.

Wetland sedge-rush ground seep
A permanently saturated area of alluvial Newark silt loam soils, where it is too wet for gentians to grow, is located at the extreme southwestern edge of the macroplot contiguous to an entranceway gravel road. This alluvial floodplain habitat is subjected to annual winter and spring floods from Stillwater Branch. Wetland graminoid associates include taxa of the Cyperaceae, *Carex frankii*, *C. lurida*, *C. vulpinoidea*, *Cyperus flavescens*, *Scirpus atrovirens*, and *S. pendulus*, the Juncaceae, *Juncus acuminatus*, *J. dudleyi*, *J. effusus* subsp. *solutus*, and *J. torreyi*, and Poaceae, *Dichanthelium polyanthes*, *Glyceria striata*, and two annual Asian invasives, *Arthraxon hispidus* and *Microstegium vimineum*. Characteristic wetland dicot species are *Agrimonia rostellata*, *Amphicarpaea bracteata*, *Bidens polylepis*, *Conoclinum coelestinum*, *Eupatorium perfoliatum*, *Eutrochium fistulosum*, *Impatiens capensis*, *Lobelia siphilitica*, *Ludwigia alternifolia*, *Lycopus virginicus*, *Mimulus alatus*, *Salvia lyrata*, and *Samolus parviflorus*. *Salix nigra* and *Sambucus canadensis* are indicator woody species. Facultative and obligate wetland plants are generally restricted to this ground seep habitat (Appendix 1, 2).

Mesic prairie inclusion meadow
Robison et al. (1995) described the mesic prairie community, soils, and indicator plants in the North Central states (Indiana, Iowa, Minnesota, Missouri, Nebraska, Ohio). In those states, *Gentiana flavida* is characterized as "competition sensitive," i.e., it is not able to compete (shade intolerant) and declines or dies out among competition from native weedy and alien (exotic) species. Mesic prairie sites typically have surface drainage where water does not collect in the loam soils (Robison et al.

1995). We classify the largest habitat where approximately 72% of the *Gentiana flavida* population is found as the mesic prairie inclusion meadow (Figure 1, 3). At Jean's Glade, several prairie remnants or prairie relics inhabiting the mesic prairie inclusion meadow are characteristic of Kentucky and North Central states mesic prairies.

Throughout the mesic prairie inclusion meadow, Newark silt loam soils intergrade into Shrouts silt clays of the hardwood-red cedar forest edge habitat. Several prairie taxa grow among characteristic old-field and disturbed sites. The mesic meadow transitions into the wetland seep habitat on the near level floodplain below and above into the subxeric rocky outcrop of the mixed hardwoods-red cedar forest edge lower slope. The meadow has numerous rocky woodland taxa interspersed by varying frequency and relative abundance.

Several mesic tallgrass prairie taxa are scattered throughout this meadow habitat. Moreover, most of these prairie remnants have a low frequency within the 1 m^2 quadrats (Appendix 1) and are rare, scarce, or infrequent in relative abundance in the macroplot (Appendix 2). Within the gentian macroplot, characteristic prairie species of moist calcareous meadows, glades, and barrens include *Asclepias tuberosa*, *A. verticillata*, *Astranthium integrifolium*, *Carex granularis*, *Chamaecrista fasciculata*, *Echinacea purpurea*, *Eryngium yuccifolium*, *Eupatorium altissimum*, *Euphorbia corollata*, *Fragaria virginiana*, *Gaura biennis*, *Gentianella quinquefolia*, *Lithospermum canescens*, *Lobelia siphilitica*, *L. spicata*, *Manfreda virginica*, *Matelea obliqua*, *Monarda fistulosa*, *Phlox glaberrima*, *Physostegia virginiana*, *Ratibida pinnata*, *Rudbeckia hirta*, *Schizachyrium scoparium*, *Silphium trifoliatum*, *Thalictrum revolutum*, and *Zizia aurea* (Appendix 2).

Many mesic to subxeric taxa characteristic of old-field colonizers exhibit a weedy habit in the meadow. Characteristic native weedy taxa include *Agrimonia rostellata*, *Ambrosia artemisiifolia*, *Calystegia sepium*, *Carex hirsutella*, *Conoclinum coelestinum*, *Desmodium glabellum*, *D. paniculatum*, *Dichanthelium clandestinum*, *Erigeron philadelphicus*, *Geum canadense*, *Leersia virginiana*, *Lysimachia lanceolata*, *Muhlenbergia sylvatica*, *Panicum anceps*, *Potentilla simplex*, *Sisyrinchium angustifolium*, *Solidago altissima*, *S. nemoralis*, *Symphotrichum shorti*, *S. pilosum*, *Tridens flavus*, *Verbesina alternifolia*, and *Vernonia gigantea*. *Rubus argutus* and *R. flagellaris* are interspersed throughout the meadow (Appendix 1, 2). The gentian population is in danger from the severe-threat invasives *Arthraxon hispidus*, *Microstegium vimineum*, and *Schedenorus arundinaceus*. Other severe-threat or significant-threat invasive taxa are *Celastrus orbiculatus*, *Daucus carota*, *Dioscorea polystachya*, *Glechoma hederacea*, *Lonicera japonica*, *Melilotus alba*, *M. officinalis*, and *Poa compressa*. Smith (1994) noted that the greatest non-native threat to *Gentiana flavida* in Arkansas was loss of habitat due to invasive cool-season grasses, especially *Schedonorus arundinaceus*.

In the moist prairie inclusion meadow, many woody plants with notable relative frequency are volunteering from the subxeric mixed hardwood-red cedar rocky forest edge even with current seasonal maintenance of cutting back shrubs and tree saplings. Woody vines, *Campsis radicans*, *Lonicera japonica*, *Parthenocissus quinquefolia*, *Toxicodendron radicans*, and shrubs, *Corylus americana*, *Rhamnus caroliniana*, *Rhus aromatica*, *Rosa carolina*, *R. setigera*, and *Viburnum rufidulum*, are important colonizers. Native tree seedlings and saplings established in the prairie inclusion meadow include *Acer saccharum*, *Carpinus caroliniana*, *Carya ovata*, *Celtis occidentalis*, *Cercis canadensis*, *Cornus florida*, *Fagus grandifolia*, *Fraxinus americana*, *F. quadrangulata*, *Juniperus virginiana*, *Liriodendron tulipifera*, *Pinus virginiana*, *Quercus alba*, *Q. imbricaria*, *Q. muhlenbergii*, *Q. rubra*, and *Robinia pseudoacacia* (Appendix 1, 2). The gentian population remains in severe jeopardy due to the continuous encroachment of the woody taxa shading out existing individuals in the absence of fire.

Subxeric mixed hardwood-red cedar forest edge

The mixed hardwood-red cedar forest edge is composed of Shrouts calcareous silt clay soils with Silurian shale and dolomite outcrops on a southwest-trending rocky lower slope. Numerous herbs and woody plants that thrive on calcareous substrates are established with soil moisture conditions varying from mesic to subxeric (Figure 1). *Gentiana flavida* occupies about 28% of the forest edge. The highest species richness is present in the forest edge stand as it is actively encroaches into the moist gentian prairie inclusion meadow.

The largely shaded moist-dry or subxeric habitat is the only location for four rare to scarce ferns, *Asplenium platyneuron*, *Botrypus virginianus*, *Polystichum acrostichoides*, and *Sceptridium dissectum*, and a rare orchid, *Spiranthes tuberosa*. Native perennial herbs among the dolomitic shale outcrops include *Agrostis perennans*, *Allium cernuum*, *Anemone virginiana*, *Arnoglossum atriplicifolium*, *Bromus pubescens*, *Carex amphibola*, *C. blanda*, *C. willdenowii*, *Cunila origanoides*, *Dichanthelium bosci*, *D. commutatum*, *Elymus hystrix*, *Endodeca serpentaria*, *Erigeron pulchellus*, *Galium circaezans*, *Helianthus microcephalus*, *Houstonia canadensis*, *Lespedeza repens*, *Lysimachia quadrifolia*, *Packera obovata*, *Penstemon digitalis*, *Podophyllum peltatum*, *Rudbeckia fulgida*, *R. triloba*, *Sanicula odorata*, *Scutellaria nervosa*, *Solidago caesia*, *Smallanthus uvedalius*, *Symphotrichum patens*, *Thaspium chapmanii*, *Uvularia perfoliata*, and *Viola hirsutula* (Appendix 2). Non-native or exotic naturalized and invasive species in the forest edge are typically those found in the mixed prairie inclusion meadow.

The subxeric mixed hardwood-red cedar forest edge comprises the woody vines, shrubs, subcanopy and canopy trees in the forested environs of Jean's Glade. Native indicator calciphile trees in Shrouts and integrading Newark silt loams include *Acer saccharum*, *Carya ovata*, *Celtis occidentalis*, *C. tenuifolia*, *Cercis canadensis*, *Fraxinus americana*, *F. quadrangulata*, *Juglans nigra*, *Juniperus virginana*, *Prunus serotina*, *Quercus muhlenbergii*, *Robinia pseudoacacia*, and *Ulmus americana*. Other important subcanopy and canopy trees are *Carpinus caroliniana*, *Carya cordiformis*, *Cornus florida*, *Fagus grandifolia*, *Liriodendron tulipifera*, *Ostrya virginiana*, *Pinus virginiana*, *Quercus alba*, *Q. rubra*, *Q. velutina*, and *Ulmus rubra*. Woodland shrubs are *Corylus americana*, *Lindera benzoin*, *Rhamnus carolinana*, *Rhus aromatica*, *Rosa carolina*, and *Viburnum rufidulum*. Important native lianas are *Campsis radicans*, *Parthenocissus quinquefolia*, *Smilax bona-nox*, *Toxicodendron radicans*, and *Vitis aestivalis*.

Braun (1950) recorded *Juniperus virginiana* and *Cercis canadensis* as dominant tree species of limestone secondary forest communities where relic prairie species were present. Rhoades et al. (2005) reported soils, habitat types, and woody plant composition in forest vegetation across grass and forb glade-forest ecotones of the Crooked Creek Barrens State Nature Preserve, in Lewis County, Kentucky. The Preserve has calcareous soils from Silurian shale and dolomite of the Crab Orchard Formation, and is located in the extreme Western Allegheny Plateau of Woods et al. (2002). *Juniperus virginiana* had the highest density within the glade interior and glade edges and was important in the forest edge and forest interior. *Cercis canadensis* and *Fraxinus americana* were first and third in density of the forest edge, and *Fraxinus americana* and *Cercis canadensis* had the highest density in the forest interior (Rhoades et al. 2005). Rhoades et al. (2005) also concluded that the locally rare prairie plants of this Preserve were threatened by land conversion, land degradation, woody plant encroachment, and non-native invasives. Jean's Glade has similar calcareous soils of the Silurian System Crab Orchard Formation within the Western Allegheny Plateau, non-native invasives, and also comprises a comparable *Juniperus-Quercus-Fraxinus-Ulmus-Cercis* forest association to Crooked Creek Barrens State Nature Preserve.

Relative frequency

A total of 143 species, representing 28 families, were present within the 30 quadrats (Appendix 1), comprising 67.77% of the total species present in the macroplot. An additional 68

species occurred within the macroplot boundary but not in quadrats. *Toxicodendron radicans, Amphicarpaea bracteata*, *Microstegium vimineum*, *Desmodium paniculatum*, *Parthenocissus quinquefolia*, *Schedonorus arundinaceus*, *Thalictrum revolutum*, *Fragaria virginiana*, and *Lonicera japonica*, had a relative frequency of 40% or greater. Seventeen species had a relative frequency of at least 30%, 33 species at least 20%, and 63 species at least 10% relative frequency (Appendix 1). An additional 89 species were recorded with less than 10% relative frequency.

Relative abundance
        Within the macroplot, only three invasive grasses, *Arthraxon hispidus*, *Microstegium vimineum*, and *Schedonorus arundinaceus* were Abundant (A) in relative abundance (Appendix 2). The lack of additional species in this category, however, is not surprising considering the relatively small area of the macroplot.   A total of 73 species (34.59% of recorded species) were either Occasional (O) or Frequent (F). Of the species in these two categories, there were two gymnosperms, one primitive angiosperm, 19 monocots, and 51 dicots. For species recorded as O or F, 62 occurred in the 1 m^2 quadrats (Appendix 2). Twenty-five species were recorded as being Rare (R): two ferns, six monocot, and 17 dicot species. No species with an R designation occurred in more than one of the 30 (1 m^2) quadrats. Sixty-eight species (32.23% of recorded species) identified in the macroplot did not appear in any of the individual quadrats. This inconsistent data is a result of the sampling timeframes. The macroplot vascular plant survey accounted for species present during all seasons of growth from spring through autumn. The 30 (1 m^2) quadrat survey, however, took place during autumn of September 2013, when the gentian population was at its flowering peak. Thus, a number of the spring and summer species present in the macroplot would have not been observed in the quadrats as they had already undergone senescence and disappeared.

Percent foliar cover
        Gentians were present in 47 of the 100 (1 m^2) non-random quadrats within the macroplot. Of these quadrats, only five were represented by more than 15% gentian foliar coverage (plots that contained genets with several ramets). The majority of quadrats represented very low coverage as 30 out of 47 contained less than 5% foliar coverage. For the quadrats with gentians present, the species represented a mean foliar coverage of only 8.18%; this data concurs with other observations. Wood and Weaver (1982) reported native *Gentiana* species are never a dominant species in the various plant communities that they inhabit.

Insolation effects on plant height
        The effects of full sun, partial shade, and canopy shade on gentian height have been observed in the field (Pringle 1963; Hilty 2008; Bebeau 2014). A total of 55 ramets were measured for height under full sun, partial shade, and total canopy shade. Plants in full sun reached an average height of 73.09 cm, those in partial shade, 56.68 cm, and those under full shade, 43.28 cm. Plants under full shade did not grow as tall as those that were not shaded at all, differing by over 30 cm in average height. In 2016, three of the 15 ramets measured in 2015 under total shade could not be located and, most likely, had perished. Genets of all ramets measured in full sun or partial shade in 2015 were relocated in 2016. Moreover, cream gentians do not thrive as well under total shaded areas compared to partial shade or full sun conditions. Leaf colors were dark green in shaded habitats, olive-green in full sun, and greenish-yellow when strongly bleached by the sun. These observations follow those reports by Hilty (2008) and Bebeau (2014).

Floristic summary
        The vascular plants of Jean's Glade comprise 211 species in 156 genera from 69 families (Table 1). Clade sections consist of four ferns, two gymnosperms, three magnoliids, 46 monocots, and 156 dicots (Table 1). Nineteen non-native naturalized taxa are present with 16 severe-threat or significant-threat invasives. A total of 161 are herbaceous (38 graminoids and 123 forbs) and 50 are woody (33 trees, 5 shrubs, and 12 lianas).   The largest families in species are Asteraceae (36),

Poaceae (22), Cyperaceae, and Fabaceae (12 each). Sixteen invasive taxa comprise 7.58% of the 211 species. Invasive grasses, *Arthraxon hispidus*, *Microstegium vimineum*, and *Schedonorus arundinaceus*, are the most severe-threat taxa. *Celastrus orbiculatus*, *Dioscorea polystachya*, *Glechoma hederacea*, and *Lonicera japonica*, are also important severe-threat species (Appendix 1, 2).

Table 1. Taxonomic distribution of vascular plants of Jean's Glade, Madison Co., Kentucky.

Clade	Family	Genera	Species	Native	Non-native	Invasive	Species %
Ferns	3	4	4	4	0	0	1.90
Gymnosperms	2	2	2	2	0	0	0.95
Magnoliids	3	3	3	3	0	0	1.42
Monocots	11	28	46	40	6	5	21.80
Dicots	50	119	156	143	13	11	73.93
Total:	69	156	211	192	19	16	100.00

CONCLUSIONS

A qualitative and quantitative ecological study of the gentian population emphasized relative frequency, relative abundance, gentian foliar cover, gentian height, and a comprehensive vascular plant survey.

1. Jean's Glade has a stable, healthy population of 268 gentian genets, many with several ramets, that occur within two habitats: (a) an open, highly insolated Mesic Prairie Inclusion Meadow and (b) a rocky lower slope at a Subxeric Mixed Hardwood-Red Cedar Forest Edge.

2. The vascular flora of Jean's Glade has significantly high species richness for a small 0.11 ha site (59 families, 156 genera, and 211 specific and infraspecific taxa). The 211 species represents 8.12% of the total 2600 species that Jones (2005) listed for Kentucky. Nineteen non-native species are documented; three are naturalized while 16 are severe-threat or significant-threat invasives. Vascular species include 161 herbaceous (38 graminoids and 123 forbs) and 50 woody (33 trees, 5 shrubs, and 12 lianas).

3. Cream gentians exhibited low foliage coverage with a mean of 8.18 percent for genets and their corresponding ramets. Gentian height measurements under various insolation revealed greater plant height under full sun, a lesser height under partial shade, and the least height and survival under total overstory shade. Data indicate a shade-intolerant or competition-sensitive taxon adapted to open, sunny habitats, i.e., mesic prairie inclusion meadow.

4. Physical and biological parameters are strongly associated with the presence of Jean's Glade gentian population and prairie species: Silurian dolomite and shale substrate, calcareous neutral to mildly alkaline (mean 7.20–7.35 pH). Newman and Shrouts soils, essential temperature-moisture regimes, and the calciphile indicator prairie remnants.

5. This gentian population compellingly merits preservation due to its endangered status in Kentucky. Three major concerns exist regarding the continuation of a healthy gentian population and survival of the other indicator mesic prairie remnants: (a) the advent and spread of severe-threat and significant-threat exotic invasive taxa; (b) management and control of woody plants encroachment from the forest edge by cutting and use of fire; and (c) an actual danger of future herbicide-spraying along a powerline corridor that passes directly through the macroplot.

6. The cream gentian population in Madison County appears to be similar to four Kentucky county populations (Lewis, Nicholas, Rowan, Robertson) where gentians have been reported from past observations by the KSNPC (2017). Our comparative inference is largely based on sparse occurrence record literature, without voucher specimens, and a meager few herbarium specimens documented to date. Similar physical and biological parameters exist in these five populations, all of which are situated within the Outer Bluegrass, Inner Bluegrass, and Hills of the Bluegrass Ecoregions of the Interior Plateau, or the Knobs Region of the Western Allegheny Plateau of Woods et al. (2002).

ACKNOWLEDGEMENTS

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Appendix 1. Relative frequency from 30 (1 m^2) quadrats in Jean's Glade, Madison Co., Kentucky.

Family	Species	Absolute Frequency	Relative Frequency %
Gentianaceae	*Gentiana flavida*	30	100.00
Anacardiaceae	*Toxicodendron radicans*	22	73.33
Fabaceae	*Amphicarpaea bracteata*	17	56.67
Poaceae	**Microstegium vimineum*	16	53.33
Fabaceae	*Desmodium paniculatum*	15	50.00
Vitaceae	*Parthenocissus quinquefolia*	15	50.00
Poaceae	**Schedonorus arundinaceus*	14	46.67
Ranunculaceae	*Thalictrum revolutum*	13	43.33
Rosaceae	*Fragaria virginiana*	12	40.00
Caprifoliaceae	**Lonicera japonica*	12	40.00
Fabaceae	*Chamaecrista fasiculata*	11	36.67
Fabaceae	*Desmodium glabellum*	11	36.67
Asteraceae	*Solidago altissima*	11	36.67
Apiaceae	**Daucus carota*	10	33.33
Asteraceae	*Arnoglossum atriplicifolium*	9	30.00
Bignoniaceae	*Campsis radicans*	9	30.00
Oleaceae	*Fraxinus americana*	9	30.00
Rosaceae	*Agrimonia rostellata*	8	26.67
Convolvulaceae	*Calystegia sepium*	8	26.67
Fabaceae	*Cercis canadensis*	8	26.67
Poaceae	*Dichanthelium bosci*	8	26.67
Asclepiadaceae	*Matelea obliqua*	8	26.67
Apiaceae	*Sanicula odorata*	8	26.67
Rosaceae	*Geum canadense*	7	23.33
Pinaceae	*Pinus virginiana*	7	23.33
Rosaceae	*Potentilla simplex*	7	23.33
Fagaceae	*Quercus rubra*	7	23.33
Asteraceae	*Vernonia gigantea*	7	23.33
Poaceae	*Dichanthelium clandestinum*	6	20.00
Euphorbiaceae	*Euporbia corollata*	6	20.00
Asteraceae	*Packera obovata*	6	20.00
Lamiaceae	**Prunella vulgaris*	6	20.00
Asteraceae	*Smallanthus uvedalius*	6	20.00
Cyperaceae	*Carex blanda*	5	16.67
Asteraceae	*Conoclinum coelestinum*	5	16.67
Cupressaceae	*Juniperus virginiana*	5	16.67
Fabaceae	*Lespedeza repens*	5	16.67
Boraginaceae	*Lithospermum canescens*	5	16.67
Ulmaceae	*Ulmus rubra*	5	16.67
Asteraceae	*Bidens polylepis*	4	13.33
Poaceae	*Elymus hystrix*	4	13.33
Asteraceae	*Eutrochium fistulosum*	4	13.33
Lamiaceae	**Glechoma hederacea*	4	13.33

Lamiaceae	*Scutellaria nervosa*	4	13.33
Iridaceae	*Sisyrinchium angustifolium*	4	13.33
Asteraceae	*Symphyotrichum pilosum*	4	13.33
Apiaceae	*Thaspium chapmanii*	4	13.33
Poaceae	**Arthraxon hispidus*	4	13.33
Rosaceae	*Agrimonia parviflora*	3	10.00
Asteraceae	*Astranthium integrifolium*	3	10.00
Cyperaceae	*Carex hirsutella*	3	10.00
Cornaceae	*Cornus florida*	3	10.00
Betulaceae	*Corylus americana*	3	10.00
Poaceae	*Dichanthelium commutatum*	3	10.00
Oleaceae	*Fraxinus quadrangulata*	3	10.00
Asteraceae	*Helianthus microcephalus*	3	10.00
Asteraceae	***Leucanthemum vulgare*	3	10.00
Campanulaceae	*Lobelia siphilitica*	3	10.00
Berberidaceae	*Podophyllum peltatum*	3	10.00
Rhamnaceae	*Rhamnus caroliniana*	3	10.00
Rosaceae	*Rosa carolina*	3	10.00
Asteraceae	*Solidago caesia*	3	10.00
Vitaceae	*Vitis aestivalis*	3	10.00

28 families, 143 species in 30 (1 m^2) quadrats; an additional 63 species are less than 10% frequency.

 (*) Naturalized taxon; (**) Invasive pest plant taxon (KY-EPPC 2013)

Appendix 2. Vascular plants of Jean's Glade, Madison Co., Kentucky.

Family	Species	Absolute Frequency	Relative Abundance
MONILOPHYTA (FERNS)			
ASPLENIACEAE			
Asplenium playneuron (L.) B.S.P. *13-625*		-	S
DRYOPTERIDACEAE			
Polystichum acrostichoides (Michx.) Schott *14-127*		-	S
OPHIOGLOSSACEAE			
Botrypus virginianus (L.) Holub *14-123; 17-212*		-	R
Sceptridium dissectum (Spreng.) Lyon *13-636*		1	R
AGROGYMNOSPERMAE (EXTANT GYMNOSPERMS)			
CUPRESSACEAE			
Juniperus virginiana L. *13-563*		5	O
PINACEAE			
Pinus virginiana Mill. *13-540*		7	O
MAGNOLIIDS AND PRIMITIVE ANGIOSPERMS			
ARISTOLOCHIACEAE			
Endodeca serpentaria (L.) Raf. *13-491; 13-616*		1	S

LAURACEAE
    Lindera benzoin (L.) Blume *13-553*   1   I
MAGNOLIACEAE
    Liriodendron tulipifera L. *13-551*   -   O

MONOCOTYLEDONAE ANGIOSPERMS

AGAVACEAE
    Manfreda virginica (L.) Salisb. ex Rose *13-639; 14-363*   -   R
ALLIACEAE
    Allium cernuum Roth *13-476; 14-564*   2   I
AMARYLLIDACEAE
    *Narcissus pseudonarcissus L. *17-43*   -   S
COLCHICACAE
    Uvularia perfoliata L. *13-535; 17-224*   -   S
CYPERACEAE
    Carex amphibola Steud. *14-162*   2   O
    Carex blanda Dewey *14-152; 17-220*   5   O
    Carex frankii Kunth *14-361*   -   S
    Carex granularis Muhl. ex Willd. *14-180*   -   O
    Carex hirsutella Mackenzie *14-207; 17-205*   3   O
    Carex lurida Wahlenb. *14-158; 17-223*   -   O
    Carex vulpinoidea Michx. *14-166*   -   O
    Carex willdenowii Schkuhr. ex Willd. *14-156*   1   I
    Cyperus flavescens L. *13-449; 17-483*   -   S
    Cyperus strigosus L. *14-561*   -   R
    Scirpus atrovirens Willd. *13-444; 14-226*   -   O
    Scirpus pendulus Muhl. ex Elliott. *13-463; 14-228* -   O
DIOSCOREACEAE
    **Dioscorea polystachya Turcz. *13-537*   1   I
IRIDACEAE
    Sisyrinchium angustifolium Mill. *14-182*   4   I
JUNCACEAE
    Juncus acuminatus Michx. *14-227*   -   R
    Juncus dudleyi Wiegand *14-230; 14-366*   -   O
    Juncus effusus L. ssp. *solutus* (Fern. & Wieg.) Hämet-Ahti. *14-224* -   O
    Juncus torreyi Coville *13-448*   -   S
ORCHIDACEAE
    Spiranthes tuberosa Raf. *17-473*   -   R
POACEAE
    *Agrostis perennan*s (Walt.) Tuckerman *14-568*   -   S
    **Arthraxon hispidus (Thunb.) Makino *14-566*   4   A
    Bromus pubescens Muhl. ex Willd. *14-206*   1   I
    Danthonia spicata (L.) P. Beauv. ex Roemer & Schultes *17-214* 4   O
    Dichanthelium bosci (Poir.) Gould & Clark. *13-516* 8   O
    Dichanthelium acuminatum (Sw.) Gould & Clark *17-222* -   I
    Dichanthelium clandestinum (L.) Gould *13-524*   6   O
    Dichanthelium commutatum (Schultes) Gould *14-144* 3   I
    Dichanthelium polyanthes (Schultes) Mohlenbrock *14-365* -   R
    Elymus hystrix L. *14-225*   4   O
    Elymus macgregori Brooks & Campbell *14-364*   -   R
    Glyceria striata (Lam.) Hitchc. *14-173*   2   I
    Leersia virginica Willd. *13-513*   2   O

**Microstegium vimineum* (Trin.) A. Camus *13-626*	16	A
Muhlenbergia sylvatica (Torr.) Torr. ex A. Gray *13-533; 17-474*	2	O
Panicum anceps Michx. subsp. *anceps 13-462*	1	O
Panicum flexile (Gattinger) Scribn. *13-608; 14-560*	1	I
Paspalum pubiflorum Rupr. ex Fournet *13-615; 14-563*	2	O
**Poa compressa* L. *14-150*	2	I
**Schedonorus arundinaceus* (Schreb.) Dumort *14-171*	14	A
Schizachyrium scoparium (Michx.) Nash *13-532; 17-472*	2	I
Tridens flavus (L.) Hitchc. *13-644*	-	O

SMILACACEAE

Smilax bona-nox L. *02-395; 17-219*	-	S

DICOTYLEDONAE ANGIOSPERMS

ACANTHACEAE

Ruellia caroliniensis (J.F. Geml.) Steud. *14-205*	1	I
Ruellia strepens L. *13-628; 14-229*	2	I

ADOXACEAE

Sambucus canadensis L. *13-612*	-	R
Viburnum rufidulum Raf. *13-556*	2	I

ALTINGIACEAE

Liquidambar styraciflua L. *17-201*	-	R

ANACARDIACEAE

Rhus aromatica Aiton *13-559; 14-161*	2	I
Toxicodendron radicans (L.) Kuntze *13-466; 14-157*	22	F

APIACEAE

Cryptotaenia canadensis (L.) DC. *14-214*	2	S
**Daucus carota* L. *13-473; 17-470*	10	O
Eryngium yuccifolium Michx. *13-450*	2	S
Sanicula odorata (Raf.) Pryer & Phillippe. *14-217; 17-211*	8	O
Thaspium chapmanii (Coult. & Rose) Small *13-493; 17-216*	4	O
Zizia aurea (L.) W.D.J. Koch *14-147; 17-215*	4	I

APOCYNACEAE

Apocynum cannabinum L. *13-442*	1	I
Asclepias tuberosa L. *14-220*	-	R
Asclepias verticillata L. *02-397*	-	R
Matelea obliqua (Jacq.) Woods. *13-514; 14-153*	8	O

ASTERACEAE

Ambrosia artemisiifolia L. *13-479*	9	F
Ambrosia trifida L. *13-461*	2	I
Arnoglossum atriplicifolium (L.) H.E. Robins. *02-394; 13-528*	3	I
Astranthium integrifolium (Michx.) Nutt. *14-143*	3	O
Bidens polylepis S.F. Blake *13-496; 13-630*	4	O
Cirsium discolor (Muhl. ex Willd.) Spreng. *13-471; 14-351*	-	S
Conoclinum coelestinum (L.) DC. *13-517; 14-567*	5	O
Echinacea purpurea (L.) Moench *13-465*	-	S
Erigeron philadelphicus L. *14-140*	2	I
Erigeron pulchellus Michx. *14-149*	1	S
Eupatorium altissimum L. *13-490; 13-606*	1	I
Eupatorium perfoliatum L. *13-477*	1	I
Eutrochium fistulosum (Barratt) Lamont *13-446*	4	O
Helianthus microcephalus Torr. & A.Gray. *13-515*	3	I
Heliopsis helianthoides (L.) Sweet *13-487*	3	O

Lactuca canadensis L. *13-454*	-	S
**Leucanthemum vulgare* Lam. *14-159*	3	I
Packera obovata (Muhl. ex Willd.) Weber & A.Löve *14-146; 17-50*	6	I
Ratibida pinnata (Vent.) Barnhart *13-460*	1	S
Rudbeckia fulgida Aiton *13-485; 14-352*	9	O
Rudbeckia hirta L. *14-352*	-	I
Rudbeckia triloba L. *14-353; 17-482*	8	O
Silphium trifoliatum L. *13-633*	2	O
Smallanthus uvedalius (L.) Mackenzie ex Small *13-470*	6	I
Solidago altissima L. *13-617*	11	F
Solidago caesia L. *13-611*	3	I
Solidago nemoralis Ait. *13-492*	2	I
Symphotrichum dumosum (L.) Nesom *13-610*	-	I
Symphyotrichum lateriflorum (L.) A. & D. Löve *13-631*	1	O
Symphyotrichum patens (Ait.) Nesom *13-521*	1	I
Symphyotrichum pilosum (Willd.) Nesom *13-618*	4	O
Symphotrichum shortii (Lindl.) Nesom *13-642; 17-477*	2	O
Symphotrichum undulatum (L.) Nesom *13-641; 17-484*	2	I
**Taraxacum officinale* Wiggers. *17-49*	-	R
Verbesina alternifolia (L.) Britton ex Kearney *13-609; 17-479*	4	I
Vernonia gigantea (Walt.) Branner & Coville *13-447*	7	O
BALSAMINACEAE		
Impatiens capensis Meerb. *13-468*	-	F
BERBERIDACEAE		
Podophyllum peltatum L. *14-131; 17-53*	3	O
BETULACEAE		
Carpinus caroliniana Walt. *13-561*	2	O
Corylus americana Walt. *13-634*	3	I
Ostrya virginiana (Mill.) K. Koch. *14-367*	2	I
BIGNONIACEAE		
Campsis radicans (L.) Seem. ex Bureau *13-555*	9	O
BORAGINACEAE		
Lithospermum canescens (Michx.) Lehm. *14-137*	5	I
BRASSICACEAE		
***Barbarea vulgaris* Ait. *17-51*	-	R
CAMPANULACEAE		
Campanula americana L. *13-457; 14-354*	-	R
Lobelia inflata L. *13-643*	1	S
Lobelia siphilitica L. *13-459; 17-000*	2	O
Lobelia spicata Michx. *02-393; 13-523*	3	S
CANNABINACEAE		
Celtis occidentalis L. *13-546*	1	I
Celtis tenuifolia Nutt. *13-622*	1	S
CAPRIFOLIACEAE		
***Lonicera japonica* Thunb. *13-607; 17-207*	11	F
CELASTRACEAE		
***Celastrus orbiculatus* Thunb. *13-541; 17-208*	2	O
CONVOLVULACEAE		
Calystegia sepium (L.) R. Br. *13-441; 14-359*	8	O
Cuscuta coryli Engelm. *17-469*	-	R

CORNACEAE
 Cornus drummondii C.A. Mey. *14-565*   - R
 Cornus florida L. *13-545; 17-47*   3 I
EBENACEAE
 Diospyros virginiana L. *13-566*   1 S
EUPHORBIACEAE
 Euphorbia corollata L. *13-474; 14-355*   6 I
FABACEAE
 Amphicarpaea bracteata (L.) Fernald *13-469; 17-475* 17 F
 Cercis canadensis L. *13-549; 17-46*   8 O
 Chamaecrista fasiculata (Michx.) Greene *13-480; 14-358* 11 O
 Desmodium glabellum (Michx.) DC. *13-489* 11 O
 Desmodium paniculatum (L.) DC. *13-499; 14-562* 15 O
 Lespedeza repens (L.) Bart. *13-453*   4 I
 **Medicago lupulina* L. *14-170; 17-209*   - S
 **Melilotus alba* Medik. *13-451*   - S
 **Melilotus officinalis* (L.) Lam. *17-206*   - S
 Robinia pseudoacacia L. *13-564*   2 O
 **Trifolium pratense* L. *14-175; 17-476*   1 I
 **Vicia sativa* L. ssp. *nigra* (L.) Ehrh. *14-133; 17-210* - S
FAGACEAE
 Fagus grandifolia Ehrend. *13-558*   1 I
 Quercus alba L. *13-613*   2 I
 Quercus falcata Michx. *17-202*   - S
 Quercus imbricaria Michx. *13-565*   1 S
 Quercus muhlenbergii Engelm. *13-554*   2 I
 Quercus rubra L. *13-548*   7 O
 Quercus velutina Lam. *13-544*   2 I
GENTIANACEAE
 Gentiana flavida A.Gray *02-392; 12-1144; 17-480* 30 F
 Gentianella quinquefolia (L.) Small *12-1146*   2 S
 Sabatia angularis (L.) Pursh *14-356*   - R
JUGLANDACEAE
 Carya cordiformis (Wangenh.) K. Koch *13-568*   - S
 Carya ovata (Mill.) K. Koch *13-621*   - I
 Juglans nigra L. *13-619*   1 R
LAMIACEAE
 Collinsonia canadensis L. *13-536*   1 I
 Cunila origanoides (L.) Britton *13-443*   2 I
 **Glechoma hederacea* L. *13-520*   4 F
 Lycopus virginicus L. *13-475*   - I
 Monarda fistulosa L. *13-464*   1 I
 Physostegia virginiana (L.) Benth. *13-455; 14-362* 6 O
 Prunella vulgaris L. *13-482; 14-360*   2 I
 Pycnanthemum pycnanthemoides (Leav.) Fernald *14-357* 2 O
 Salvia lyrata L. *14-135*   - I
 Scutellaria incana Biehler *17-471*   - S
 Scutellaria nervosa Pursh *14-126*   4 I
MYRSINACEAE
 Lysimachia lanceolata Walt. *13-531; 14-210*   2 I
 Lysimachia quadrifolia L. *13-623; 14-178*   8 O

OLEACEAE
    Fraxinus americana L. *13-542* — 9 — O
    Fraxinus quadrangulata Michx. *13-635* — 3 — S
ONAGRACEAE
    Gaura biennis L. *13-484; 14-569* — - — I
    Ludwigia alternifolia L. *13-452* — - — I
OROBANCHACEAE
    Pedicularis canadensis L. *13-495; 14-128* — - — I
OXALIDACEAE
    Oxalis grandis Small *13-632; 14-164* — 2 — O
PHYRMACEAE
    Mimulus alatus Aiton *13-458* — 2 — S
PLANTAGINACEAE
    Penstemon digitalis Nutt. ex Sims. *14-154; 17-221* — - — I
    Plantago rugelii Decne. *13-519* — 1 — I
PLATANACEAE
    Platanus occidentalis L. *13-638* — 1 — S
POLEMONIACEAE
    Phlox divaricata L. var. *divaricata* *17-48* — - — I
    Phlox glaberrima L. *14-163; 17-225* — - — S
    Polemonium reptans L. *17-42* — - — R
RANUNCULACEAE
    Anemone virginiana L. *13-445; 14-21* — 10 — I
    Clematis virginiana L. *13-552* — 2 — I
    Thalictrum revolutum DC. *14-168; 14-169* — 13 — F
    Thalictrum thalictroides (L.) Eames & Boivin *17-41* — - — S
RHAMNACEAE
    Rhamnus caroliniana Walt. *13-547* — 3 — I
ROSACEAE
    Agrimonia parviflora Aiton *13-467* — 3 — O
    Agrimonia rostellata Wallr. *13-478* — 8 — O
    Fragaria virginiana Dcne. *13-494* — 12 — O
    Geum canadense Jacq. *13-483* — 7 — I
    Physocarpus opulifolius (L.) Maxim. *17-200* — - — R
    Potentilla simplex Michx. *13-538; 14-136* — 7 — O
    Prunus serotina Ehrh. *13-560* — - — I
    Rosa carolina L. *13-543; 14-176* — 3 — I
    Rosa setigera Michx. *13-620; 14-213* — 2 — S
    Rubus argutus Link *13-569* — 1 — O
    Rubus flagellaris Willd. *14-125* — 2 — I
RUBIACEAE
    Galium circaezans Michx. *13-539; 14-215* — 1 — I
    Galium triflorum Michx. *14-124* — 2 — O
    Houstonia canadensis Willd. ex Roemer & Schultes. *14-148* — - — I
SALICACEAE
    Salix nigra Marsh. *14-223* — - — R
SAPINDACEAE
    Acer saccharinum L. *13-614* — - — R
    Acer saccharum Marsh. *13-562* — 2 — I
SOLANACEAE
    Solanum carolinense L. *13-529; 14-212* — 1 — R

THEOPHRASTACEAE
 Samolus parviflorus Raf. *13-481*   -   R
ULMACEAE
 Ulmus americana L. *14-231; 14-570*   2   S
 Ulmus rubra Muhl. *13-567; 14-129*   5   O
VERBENACEAE
 Verbena urticifolia L. *13-472*   -   I
VIOLACEAE
 Viola hirsutula Brainerd *17-52*   -   I
VITACEAE
 Parthenocissus quinquefolia (L.) Planch. *13-624*   15   F
 Vitis aestivalis Michx. *14-177; 17-213*   3   O

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(*) Naturalized taxon; (**) Invasive pest plant taxon (KY-EPPC 2013)